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Il était une fois une cible et un distracteur : électrophysiologie des mécanismes corticaux de l'attention visuelle en perception et en mémoire.

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Résumé

Cet ouvrage explore en trois volets des aspects du traitement attentionnel de cibles et de distracteurs visuels ainsi que leur mesures électrophysiologiques. Le premier chapitre aborde le traitement attentionnel spécifique à la cible et aux distracteurs durant une recherche visuelle. La division de la N2pc en une N_T et une P_D remet en question la théorie proposant qu'il existe systématiquement une activité attentionnelle liée à un distracteur saillant, car un distracteur vert ne provoque aucune activité latéralisée propre. Le second chapitre aborde la question de la latéralisation des structures responsables du maintient et de la récupération d'information en mémoire visuelle à court-terme. En utilisant un paradigme de latéralisation de la cible et du distracteur, il nous est possible de vérifier qu'il existe une composante latéralisée négative dans la région temporale, la TCN, propre à la cible lors du rappel en mémoire. De plus, on observe également une composante latéralisée pour le distracteur sur la partie postérieure du crâne. Ces deux éléments convergent pour indiquer qu'il existe une latéralisation des structures activées lors de la récupération de l'information en mémoire visuelle à court-terme en fonction de l'hémichamps où se trouve la cible ou le distracteur. Enfin, dans le troisième chapitre, il est question de l'effet sur le déploiement attentionnel de l'ajout de distracteurs gris de faible saillance autour de cibles potentielles. L'ajout de ces distracteurs augmente la difficulté d'identification de la cible. Cette difficulté provoque un déplacement de l'activité de la N2pc vers la fenêtre de temps associée à la composante Ptc. Un nombre plus important de distracteurs gris entraîne une plus grande proportion de l'activité à être retardée. Également, les distracteurs gris qui sont placés entre les cibles potentielles provoquent un retard plus important que les distracteurs placés hors de cette région. Au cours de cette thèse, la question de la saillance attentionnelle des différentes couleurs durant une recherche visuelle est récurente. Nous observons une plus grande saillance du rouge par rapport au vert quand ils sont distracteurs et le vert est plus difficile à distinguer du gris que le jaune.

Mots-clés : Attention, recherche visuelle, mémoire, cible, distracteur, N2pc, TCN, Ptc, couleur

Abstract

This thesis explore various aspects of attentional processing of visual targets and distractors as well as their electrophysiological expression. First, the opening chapter investigate target and distractor specific attentional processing during a visual search task. Splitting the N2pc into an NT and a PD allows us to reject the hypothesis that all salliant distractors require an attentionnal processing, since no distractor-specific lateralized activity can be observed for a lateral green distractor. After then, during the second chapter, we separate target and distractor specific activity during VSTM retrieval to explore the lateralization of memory structures. We identified a temporal lateralized negative component, the TCN, which is solely related to the retrieval of the target from VSTM. We also found a posterior distractor-related positive component. Both components suggest a lateralized activation of structures during VSTM retrieval related to the encoding hemisphere during perception. Then finally, during the third chapter, despite the absence of systematic attentional processing, we explore the effect of low salience distractors on attentional deployment during a visual search task. Inserting grey distractors around color potential targets increases the difficulty to individuate the potential targets and lead to attentional deployment delay. Increasing the number of grey distractors lead to an increased proportion of N2pc activity being delayed into the following Ptc time-window. Also, more delayed activity can be observed when grey distractors are placed between the potential targets instead of outside this region. Across this thesis, we also address the attentional salience of color as a recurent source of attentional imbalance. Red generate distractor-specific lateralized activity, while green do not and green is harder to individuate with surrounding grey distractors compared to yellow.

Keywords : Attention, visual search, VSTM, target, distractor, N2pc, TCN, Ptc, color

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Liste des abbréviations

CDA : Contralateral delay activity
: Activité tardive contralatérale

CNSW : Contralateral negative slow wave
: Onde lente négative contralatérale

EEG : Électroencephalographie

ERL : Event-related lateralization
: Potentiels latéralisés

ERP : Event-related potential
: Potentiels évoqués

HEOG : Horizontal electrooculogram
: Électroocculogramme horizontal

LAI : localized attentional interference
: Interférence attentionelle locale

N2pc : Négativité 200 ms postérieure contralatérale

N_T : Negativity related to the target
: Négativité liée à la cible

P3 : Positivité 300 ms

P_D : Positivité liée au distracteur

Ppc : Positivité postérieure contralatérale

Ptc : Positivité temporale contralatérale

RT : Response time
: Temps de réponse

SPCN : Sustained posterior contralateral negativity
: Négativité soutenue postérieure contralatérale

TCN : Temporal contralateral negativity
: Négativité temporale contralatérale

TRA : Théorie de la résolution de l'ambiguïté

VEOG : Vertical electrooculogram
: Électroocculogramme vertical

VSTM : Visual short-term memory
: Mémoire visuelle à court-terme

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Introduction

Il était une fois un monde où une seule chose pouvait exister à la fois... Aucune compétition n'existe dans la représentation du monde, aucune trace n'y demeure de ce qui s'y est passé, aucune projection n'est possible de ce qui pourrait arriver. Un humain vivant dans un tel monde sans alternatives, sans mémoire et sans futur serait bien différent de ceux que l'on connait. Ce monde bien improbable illustre à quel point les mécanismes attentionnels sont fondamentaux au fonctionnement humain dans l'univers que nous habitons. Les mécanismes attentionnels nous permettent de gérer la complexité du monde en limitant la quantité d'information disponible pour notre fonctionnement. Ceci a pour effet direct de créer deux catégories fluides désignant les différents éléments de notre représentation du monde. D'abord, les cibles sont les éléments d'information d'intérêt immédiat dans une situation et à un moment précis. En contrepartie, les distracteurs sont les autres éléments d'information qui ne font pas partie du champs d'intérêt actuel et qui peuvent interférer avec notre fonctionnement. Cet ouvrage fait un survol des effets électrophysiologiques observables liés à des cibles et des distracteurs visuels et qui permettent d'explorer les mécanismes attentionnels qui leur sont reliés.

Revenons en arrière pour définir ce qu'est l'attention et plus spécifiquement l'attention visuelle. Le terme attention se rapporte aux mécanismes impliqués dans la sélection et le traitement d'un sous-ensemble d'informations pour en améliorer le traitement. Dans le cas de l'attention visuelle, on parle d'informations d'origine visuelle, mais aussi des représentations corticales qui en découlent, tels orientations, formes, couleurs, objets, etc. L'attention est donc un outil qui nous permet de mettre en valeur une partie de l'information disponible au détriment du reste. L'attention visuelle englobe à la fois les mécanismes qui régissent la sélection (critères, modes, temps requis, étendue, forme) et ceux qui régissent le traitement de l'information (analyse des informations visuelles, durée, rétention, comparaison). La sélection attentionnelle peut elle-même se décliner en deux volets : la prise de décision (sans impliquer nécessairement qu'elle est consciente) qui désigne le choix d'une cible parmi les alternatives

disponibles et le déploiement (ou engagement) attentionnel qui consiste à mettre en place, pour le sous ensemble ciblé, les mécanismes nécessaire au traitement attentionnel. On pourrait donc présenter comme définition opérationnelle de l'attention visuelle la différence de traitement qui existe entre ce qui nous intéresse (la cible) et ce qui ne nous intéresse pas (les distracteurs), mais également les mécanismes additionnels qui permettent cette ségrégation. Malheureusement, le portrait est bien plus complexe et le calcul plus ambigüe. La compréhension des mécanismes et des facteurs attentionnel est un domaine large qui nécessite une certaine compréhension de la progression des connaissances et des théories pour bien suivre l'argumentation liée plus spécifiquement aux sujets abordés par cette thèse.

Historiquement, les premières recherches sur l'attention, notamment par Broadbent (1958) sur l'écoute dichotique, ont tenté d'établir à quel niveau de traitement parvenait l'information sensorielle avant qu'il y aie un effet attentionnel observable. L'écoute dichotique fournissait un paradigme simple pour tester empiriquement l'information perçu par des participants en leur demandant de porter attention aux sons qui étaient présentés soit à leur oreille gauche soit à leur oreille droite. La théorie de Broadbent proposait que l'attention agissait à la manière d'un filtre et qu'elle agissait avant que l'information sensorielle soit traitée pour en extraire l'information sémantique. L'information sensorielle était déposé dans une mémoire tampon d'où l'attention sélectionnait le contenu à analyser en fonction des propriétés physiques du stimulus (intensité, fréquence, timbre). Cependant, ce modèle de filtre attentionnel qui précédait tout traitement sémantique ne permettait pas d'expliquer des observations tel l'effet « cocktail party » (Cherry, 1953). Dans un environnement bruyant malgré qu'un stimulus auditif ne se distingue pas au niveau de ses propriétés physiques fondamentales, il est possible qu'il attire l'attention par son contenu, par exemple entendre son propre nom. Cet effet requiert, hors du traitement attentionnel, un certain niveau de traitement sémantique.

Pour permettre un traitement sémantique de l'information sensorielle sans attention, Treisman (1964) propose un modèle d'atténuation. Au lieu de bloquer complètement le traitement de l'information qui ne bénéficie pas de traitement attentionnel, l'attention permet d'atténuer cette information. L'accès conscient au contenu n'est possible que si un certain seuil d'activation est dépassé en raison de facteurs contextuels ou d'alerte tel le nom, les mots aggressifs ou d'avertissement. Ce modèle propose donc une sélection attentionelle tardive lors du traitement de l'information sensorielle permettant un certain niveau de traitment sémantique. En contrepartie, Deutsch et Deutsch (1963) et Norman (1968) proposent plutôt un modèle de mémoire sélective où les informations sensorielles sont complètement analysées. L'attention n'intervient qu'au moment du passage en mémoire. Les informations pertinentes sont retenues, alors que le reste est discarté. Le modèle de l'atténuation de Treisman et le modèle de la mémoire sélective de Deutsch et Deutsch proposent deux approches qui permettent un traitement de l'information suffisant pour expliquer l'effet « cocktail party ».

Les modèles proposés à cette époque relèvent d'une représentation essentiellement unidirectionnelle de la perception. L'information sensorielle progresse d'une étape d'analyse à la suivante en fonction de ses propriétés et des règles de sélection établies par le filtre attentionnel. L'analyse de l'information devient ainsi progressivement plus raffinée, passant du bas de l'échelle occupé par le traitement élémentaire des informations physiques à l'échelon supérieur occupé par l'analyse sémantique du contenu sensoriel adoptant une progression que l'on peut qualifier d'ascendante. Cette conception du traitement de l'information n'était pas partagée par Neisser (1967) qui était convaincu que la partie attentionnelle du traitement de l'information reposait essentiellement sur un travail actif de synthèse des informations sensorielles disponibles en prenant en compte les informations disponibles en mémoire et les anticipations de la personne. Un tel processus d'injection de critères et d'*a priori* à partir de centre cognitifs de plus haut niveau est qualifié de descendant. Neisser proposait un modèle séparé en deux phases. La première phase préattentive faisait une collecte des propriétés physiques fondamentales du stimulus et permettait une sélection attentionnelle sur cette base. La seconde phase attentionnelle était une activité de synthèse active qui complétait l'analyse

des éléments sélectionnés durant la première phase. Ce modèle en deux stades dont l'un préattentionnel pave la voie à la théorie attentionnelle de l'intégration des caractéristiques (Treisman et Gelade,1980; Treisman, 1988). Cette théorie propose qu'une phase préattentive fait la décomposition en cartes de caractéristiques élémentaires du stimulus perçu dans des aires spécialisées distinctes. La phase attentionnelle permet quant à elle d'accéder à ces cartes et d'en combiner les éléments.

Treisman et Gelade (1980) ont utilisé des tâche de recherche visuelle pour leurs expériences. Il s'agit d'un paradigme important en recherche sur l'attention visuelle. Ce type de tâche consiste à présenter une scène visuelle comportants plusieurs items avec des caractéristiques différentes et de demander au participant de compléter une opération sur un sous ensemble de ces items en les désignant comme cible. Ces tâches comportent donc une ou plusieurs cibles et des distracteurs. En ajoutant des distracteurs, on rend la tâche plus difficile ce qui provoque un temps de réponse proportionnellement plus lent. Il est cependant possible, en utilisant certaines caractéristiques pour définir la cible tels la couleur, la taille, l'orientation ou le mouvement, d'obtenir des temps de réponse pratiquement égaux quelque soit le nombre d'items présentés. On appelle ce type de recherche « pop-out » pour indiquer que les cibles ressortent parmi les distracteurs qui peuvent être aisément ignorés.

C'est au moment de l'émergence de ces nouveaux modèles que commence à prendre de l'ampleur la recherche sur l'attention visuelle. Celle-ci nécessite une nouvelle approche, car la sélection ne se fait pas de manière aussi tranchée qu'en audition. On peut aisément porter attention aux sons perçus par l'une ou l'autre de nos oreilles, mais ce n'est pas aussi simple pour la vision. Le champs visuel est construit par la combinaison des apports de chaque œil en un seul plan visuel. La notion de focus attentionnel avec une position et une dimension spatiale devient nécessaire. Posner (1980) est parmi les premier à s'intéresser à l'attention dans la modalité visuelle. Il propose un modèle de faisceau attentionnel d'une taille fixe qui peut être déplacé sans mouvement des yeux vers la cible attentionnelle. LaBerge (1983) obtient des

résultats qui supportent le modèle du faisceau attentionnel tout en ajoutant le raffinement que ce faisceau pouvait être ajusté en étendue en fonction des demandes de la tâche. Ainsi une tâche de lecture de mots demande une plus grande étendue du faisceau qu'une tâche d'identification de lettres. Eriksen et James (1986) viennent proposer un rafinement au modèle en proposant une lentille attentionnelle. Un faisceau attentionnel dont les ressources seraient plus concentrées lors d'un déploiement sur une petite superficie que sur une grande. Le faisceau attentionnel n'est pas incompatible avec la théorie attentionnelle de l'intégration des caractéristiques. La théorie propose une décomposition en cartes d'organisation rétinotopique qui conservent l'information spatiale. L'attention peut ainsi combiner les caractéristiques des éléments se trouvant à l'intérieur du faisceau sur chacune des cartes. Pourtant, bien que généralement acceptée, la forme en faisceau de l'attention visuelle n'est pas universellement reconnue.

Castiello et Umilta (1992) proposent quant à eux qu'il est possible de diviser l'attention visuelle. Cette position est supportée par d'autres chercheurs (Hahn & Kramer, 1998, Awh & Pashler, 2000), mais elle repose sur un certain nombre de conditions. Les principales conditions nécessaires pour un traitement attentionnel favorisant le traitement de cibles distantes sont que les positions spatiales des cibles distinctes soient connues à l'avance et qu'il n'y aie pas de distracteur qui apparaissent subitement. L'apparition subite des cibles et distracteurs est un élément important de la sélection attentionnelle comme le soulignent Jonides et Yantis (1988). L'apparition subite d'un distracteur est suffisante pour provoquer la sélection attentionnelle, ce qui viendrait briser la division du focus attentionnel. Il y a aurait donc une opposition entre la sélection imposée de façon descendante par les positions spatiales connues pour les cibles et l'influence ascendante imposée par l'apparition subite de distracteurs. Ceci nous plonge dans un autre débat.

Un autre aspect de l'attention qui demeure contesté est l'apport des facteurs ascendants et descendants à la sélection attentionnelle. D'une part, Theeuwes (1992) propose que la

sélection attentionnelle qui se produit durant la phase préattentionnelle n'est pas sous contrôle descendant pour les formes et les couleurs. La sélection se produit sur la base de la saillance relative ascendante des stimuli basée sur leur propriétés physiques. Les facteurs descendants n'entreraient en jeu que durant la phase attentionnelle. Il reconnaît toutefois que pour la sélection d'une cible à l'aide de plus d'une caractéristique (une combinaison de forme et couleur par exemple), les facteurs descendants peuvent jouer un rôle, mais cela implique également qu'une sélection de tel cibles durant la phase préattentionnelle est impossible. À l'opposé, Folk, Remington et Johnston (1992) proposent que la sélection attentionnelle est contingente au fait que les propriétés d'un stimulus correspondent aux demandes de la tâche. Un distracteur pourrait être sélectionné que s'il peut être identifié par un élément pouvant servir à sélectionner une cible. La sélection attentionnelle reposerait donc sur les influences ascendantes, mais dans le cadre de barêmes de sélection préétablis de manière descendante. Ce débat a mené au concept de mode de recherche visuel.

Bacon et Egeth (1994) viennent rafiner la position de la sélection contingente pour expliquer les résultats de Theeuwes en proposant qu'il existe des modes de recherche visuelle. La sélection visuelle serait sensible au contexte visuel pour établir un mode de recherche approprié à une tâche. Le mode le plus économique au niveau des ressources cognitives pour sélectionner une cible serait le mode par singleton. Si une cible peut être identifiée par son caractère unique sur l'une de ses caractéristiques, la recherche se déroulera de préférence en mode singleton et fera la sélection des items uniques. Dans ce mode de recherche, un distracteur unique viendra compétitionner avec la cible pour la sélection. Par contre, si le contexte ne permet pas une sélection de la cible en mode singleton, la sélection s'effectuera en mode caractéristique qui favorise la sélection basée sur les caractéristiques propre à la cible. Dans ce mode, la sélection attentionnelle est insensible aux distracteurs uniques qui ne partagent pas une caractéristique avec la cible.

Ce survol rapide de différentes théories ayant servi à expliquer le fonctionnement de l'attention visuelle, bien qu'incomplet, permet d'introduire différents concepts et questionnements qui nourissent ce domaine de recherche et qui doivent être pris en compte lors de l'interprétation des résultats expérimentaux dans le domaine. Plusieurs questions n'ont toujours pas trouvées de conclusion, ce qui rend la compréhension des différents enjeux d'autant plus important. Il est aussi important pour comprendre cet ouvrage d'avoir une compréhension des enjeux liés à l'approche électrophysiologique. Nous poursuivons donc notre survol en introduisant les bases de la recherche électrophysiologique de l'attention visuelle.

L'électroencéphalographie (EEG) permet, à l'aide d'électrodes apposées sur la surface du crâne de participants, de mesurer l'activité électrique cérébrale lors du déroulement d'une tâche expérimentale. Ainsi en faisant exécuter une tâche visuelle à un participant, il est possible de mesurer des variations d'activité électrique en fonction des différentes conditions expérimentales. À la base, le signal enregistré sur le crâne comporte une grande proportion de bruit, qu'il soit biologique ou environemental, comparé au signal d'intérêt. En plus des champs électromagnétiques ambiants, des décharges électriques musculaires, des propriétés dipolaires des yeux, le cerveau, lui-même, à tout moment, est traversé d'une panoplie de décharges électriques provenant d'activités qui n'ont rien à voir avec la tâche expérimentale en cours. Pour extraire le signal d'intérêt du bruit, une approche répandue, la méthode des potentiels évoqués (ERP, event-related potentials), consiste à faire la moyenne d'un nombre important d'essai expérimentaux correspondant à une même condition en alignant le signal mesuré sur un événement significatif de la tâche. Cette approche permet de conserver le signal, commun à tous les essais moyennés, et d'annuler le bruit, qui est aléatoire d'un essai à l'autre puisqu'il n'est pas relié à la tâche. Les effets expérimentaux peuvent donc être mesurés en tant que différences sur des courbes de potentiels mesurées à chaque électrode, mais également en tant que répartition topographique caractéristique de l'activité sur le crâne des participants en utilisant un système commun de position d'électrodes. Les périodes d'activité caractéristique visible sur les courbes de potentiels sont nommées composantes. Elles sont caractérisées par

une déflection positive ou négative dans une fenêtre de temps précise ainsi que par une topographie typique sur le crâne.

Les aires corticales visuelles chez l'humain se retrouvent à l'arrière de la tête dans le lobe occipital. Il est donc normal que, bien que l'activité électrique se propage à l'intérieur du crâne et à sa surface, les effets électrophysiologiques liée à la perception visuelle se retrouvent principalement dans les régions postérieures du crâne. Par contre, plusieurs processus attentionnels et de mémoire associés à la modalité visuelle se retrouvent dans des régions antérieures. Il est important de comprendre que l'activité mesurée à la surface du crâne représente la sommation dynamiques des potentiels électriques provenant de différente sources cérébrales. Il est donc dangereux d'inférer la source de cette activité à partir de la position sur le crâne. Toutefois, une approche électrophysiologique permet d'observer le déroulement d'une activité qui est autrement invisible. Les mesures électrophysiologiques s'ajoutent donc aux temps de réponses et au taux de succès pour décrire et comprendre les mécanismes attentionnels.

En 1994, Luck et Hillyard identifient la N2pc, une composante électrophysiologique qu'ils croient relié au filtrage attentionnel, inhibant le traitement d'informations non pertinentes qui entrent en compétition avec l'analyse d'une cible. Lorsqu'on aligne le signal avec la présentation d'un stimulus visuel, il s'agit d'une composante négative observée peu après 200 ms sur les électrodes postérieures contralatérales à une cible. Cette composante sert de tremplin à la recherche sur l'attention visuelle en électrophysiologie.

La N2pc a comme particularité qu'elle est calculée à partir de la différence de potentiel entre les électrodes contralatérales et les électrodes ipsilatérales à une cible attentionnelle latérale. On appelle ce type de représentation du signal une latéralisation évoquée (ERL, event-related lateralization). Si on considère une présentation visuelle dont le contenu de

l'hémichamp droit est une réflexion du contenu de l'hémichamp gauche, l'activité mesurée aux électrodes correspondantes du côté droit et gauche sur le crâne est égale à moins d'être modifiée par l'attention. Chacun des hémichamps visuels est représenté dans les aires visuelles controlatérales. Si on suppose que les processus lié à l'attention provoquent un changement de l'activité des aires visuelles, cette soustraction permet de faire ressortir la modification d'activité corticale latéralisée causée par l'attention lors de la présentation latérale d'une cible. Les latéralisations évoquées ont également comme avantage, en plus de soustraire l'activité équivalente pour les deux hémichamps, de masquer l'activité non correllée avec le côté où se trouve la cible, tel l'activité lié à la réponse.

Luck (1997) propose la théorie de la résolution de l'ambiguïté (TRA) pour expliquer le mécanisme attentionnel que représente la N2pc. Les aires du cortex visuel qui traitent l'information plus complexe ont des champs récepteurs plus grands que celles qui traitent l'information plus simple. Les champs récepteurs des aires complexes reçoivent de l'information d'une plus grande superficie et, par conséquent, l'information provenant d'un distracteur proche d'une cible augmente l'ambiguïté de l'information traitée. Le traitement attentionnel, incluant celui représenté par la N2pc, permet de filtrer l'effet des distracteurs au sein du focus attentionnel pour améliorer la discriminabilité de la cible.

Cependant, plusieurs études retrouvent des N2pc lors d'expériences présentant des distracteurs distants ou peu nombreux (Eimer, 1996; Brisson & Jolicoeur, 2007a) qui présentent peu de chance d'interférer avec la cible au niveau des champs récepteurs. L'alternative proposée par Eimer (1996) est que la N2pc représentait le traitement attentionnel de la cible même. Mazza, Turatto et Caramazza (2009) présentent également des résultats qui remettent en question la TRA. Ils vérifient que la distance qui sépare les distracteurs d'une cible n'affecte pas l'amplitude de la N2pc relié à la cible lorsqu'on maintient constant le nombre de distracteurs. La TRA, qui lie la taille des champs récepteurs à l'amplitude de la N2pc prédit un niveau d'ambiguïté variable en fonction de la distance. Par contre, Mazza et

collègues (2009) observent également une N2pc plus ample pour un nombre de distracteurs plus élevé. Ces résultats suggèrent bien un lien entre la N2pc et l'ambiguïté provoquée par des distracteurs, mais la taille des champs récepteurs ne semble pas être en cause.

Hilimire, Parks, Mounts et Corballis (2009, 2010) proposent une théorie d'interférence attentionnelle localisée (LAI, localized attentional interference) similaire à la TRA, mais dont l'effet est inverse sur la N2pc. La taille des champs récepteurs des aires visuelles extrastriées provoquerait une compétition latérale destructive supérieure pour des cibles et des distracteurs rapprochés. Cette compétition aurait pour effet d'observer une N2pc de plus petite amplitude lorsqu'un distracteur est proche d'une cible alors que la N2pc serait plus grande pour un distracteur plus distant de la cible. Ainsi la TRA prévoit une plus grande N2pc pour un besoin accru de discrimination avec la proximité d'un distracteur alors que la LAI prévoit une plus grande N2pc pour une distance plus grande réduisant l'interférence entre les représentations corticales de la cible et du distracteur.

Ces deux théories opposées font ressortir le fait qu'on ne sait toujours pas si la N2pc et les mécanismes attentionnels qui s'y rattachent sont liés au traitement de la cible, à l'inhibition des distracteurs ou encore aux deux à la fois. Hickey, Di Lollo et McDonald (2009) montrent qu'il existe bien de l'activité latéralisée liée uniquement au distracteur sous la forme d'une composante qu'ils nomment P_D (positivité lié au distracteur). L'essentiel de l'activité de la N2pc est cependant associée à la cible qu'on peut retrouvé dans la composante N_T (négativité lié à la cible). La N2pc serait donc la somme d'une négativité liée à la cible et d'une positivité liée au distracteur. La P_D possède une topographie similaire à la N_T sur le crâne, mais arrive à une latence plus tardive. Pour séparer l'activité propre à la cible et au distracteur, ils placent sur la ligne de séparation des deux hémichamps l'item dont ils veulent soustraire la contribution. La soustraction pour obtenir la latéralisation évoquée isole l'activité liée à l'item latéral.

Une des observations faite par Hilimire et collègues (2009, 2010) concernait une composante qu'ils ont nommé Ptc (positivité temporale contralatérale) qui suit immédiatement la N2pc. Alors que la N2pc décroit en amplitude avec la proximité accrue d'un distracteur, la Ptc croit et devient plus positive. Il est possible que l'effet observé sur la N2pc et la Ptc, pour une expérience dont la cible et le distracteur se retrouvent dans le même hémichamp, soit en fait l'apport de la P_D dont la latence chevauche les deux composantes. Malgré une certaine convergence des résultats, certains éléments de leur paradigme expérimental soulèvent des questions. L'utilisation de couleur pour la cible et le distracteur et la présence de distracteurs gris pour compléter la présentation circulaire viens compliquer l'interprétation de leur résultats. L'utilisation d'une couleur pour faire une sélection préattentionnelle pourrait mener à une taille du focus attentionnel variable entre les conditions ce qui correspondrait à une distribution différente des ressources attentionnelles selon la théorie de la lentille de Eriksen et James (1986). De plus, si on considère une taille variable du focus attentionnel, on obtient un nombre croissant de distracteurs gris dans le focus pour une distance croissante entre cible et distracteur. Le traitement attentionnel lié à ces distracteurs pourrait également avoir un effet variable sur la N2pc et la Ptc confondu avec celui de la distance.

Il semble donc que la N2pc représente de l'activité attentionnelle provenant à la fois de la cible et du distracteur, ou du moins, de l'influence du distracteur sur le traitement attentionnel de la cible. Cela n'éclaire pas pour autant quels processus attentionnels sont rattachés à la N2pc. Leblanc, Prime et Jolicœur (2008) testent à l'aide de la N2pc la théorie de la sélection contingente de l'attention. Leurs résultats montrent que seuls les distracteurs qui partagent une caractéristique avec la cible interfèrent avec la tâche et sont accompagnés d'une N2pc. En plus de supporter la vision contingente de la sélection attentionnelle, cette expérience suggère qu'il existe bien deux phases de sélection, l'une préattentionnelle et l'autre attentionnelle. La N2pc représente donc une sélection attentionnelle tardive impliquant un déploiement attentionnel. Il existerait donc un mécanisme de sélection qui précède la N2pc qui permet d'éviter un déploiement attentionnel vers un distracteur qui ne partage pas une caractéristique de la cible. Jolicœur, Brisson et Robitaille (2008) quand à eux éclairent quelque

peu les limites tardives de la N2pc en dissociant cette dernière d'une autre composante latéralisée qui la suit, la SPCN.

La SPCN (sustained posterior contralateral negativity) (Jolicœur, Sessa, Dell'Acqua et Robitaille, 2006), également obervée par Klaver, Talsma, Wijers, Heinze et Mulder (1999) sous le nom de CNSW (contralateral negative slow wave), ainsi que par Vogel et Machizawa (2004) en tant que CDA (contralateral delay activity), serait une composante qui représente l'information maintenue en mémoire visuelle à court-terme (VSTM). Cette composante latéralisée aurait une amplitude plus grande pour chaque élément en mémoire (Vogel et Machizawa , 2004). En montrant que la N2pc ne se comporte pas comme la SPCN pour un nombre supérieur d'éléments visuels en mémoire, Jolicœur et collègues (2008) proposent que l'action de la N2pc se termine à l'entrée de l'information en mémoire et que le traitement attentionnel additionnel est complété durant la SPCN. La N2pc représenterait donc le déploiement de l'attention, la sélection des cibles parmi les cibles potentielles et ferait l'extraction des informations visuelles nécessaire à l'accomplissement de la tâche. Les manipulation attentionnelles de ces informations ainsi que la sélection d'une réponse se produirait plus tardivement durant la SPCN. L'activité latéralisée de la SPCN suggère qu'il existe en VSTM un mécanisme attentionel qui encode et maintient une représentation des éléments visuels dans l'hémisphère contralatérale. La récupération de ces informations en mémoire ferait appel à des mécanismes attentionels similaire à ceux mis à contribution durant la perception. Dell'Acqua, Sessa, Toffanin, Luria et Jolicœur (2010) ont de surcroit isolé une composante latéralisée négative présente lors de la récupération d'information en VSTM qui possède des caractéristiques similaires à la N2pc, mais avec une latence et une topographie différente sur le crâne.

On observe donc aussi bien en perception qu'en mémoire des composantes électrophysiologiques représentant une portion d'activité attentionelle. Ces composantes sont des outils pour interpréter les résultats expérimentaux, mais elles sont elles-même des sources

d'interrogations et de débats. En explorant l'activité attentionelle liée aux cibles et aux distracteurs, nous nous trouvons également à chercher à clarifier l'activité qu'accompagne les différentes composantes. Cette thèse explore l'activité attentionnelle liée aux cibles et aux distracteurs sous différents aspects pour tenter de mieux la comprendre.

Tout d'abord, nous vérifions lors du premier chapitre l'hypothèse proposée par Hickey et collègues (2009) qu'il existe une composante électrophysiologique positive propre aux distracteurs lors d'une tâche de recherche visuelle. Cette composante, la P_D, serait confondu à l'activité liée à la cible lors d'une tâche de recherche visuelle typique comportant une cible dans un hémichamp visuel et un distracteur dans l'hémichamps opposé. Nous mettons à l'épreuve les résultats obtenus par Hickey et collègues (2009), car la tâche de recherche visuelle qu'ils ont utilisés comportait des facteurs confondants. Tout d'abord, le distracteur était toujours une ligne de couleur rouge ce qui aurait pu introduire des mécanismes de sélection descendants qui ne sont pas toujours en place lorsque les caractéristiques de la cible ne sont pas aussi stable. Également, la présentation visuelle n'était pas balancée entre les deux hémichamps visuels lors de l'observation de la P_D, car le distracteur n'était pas contrebalancé par un élément dans l'autre hémichamp avec des caractéristiques simililaires. Nous contournons ces facteurs confondants en utilisant un indicateur au point de fixation pour définir la couleur cible d'essai en essai et des distracteurs gris équiluminants à la cible et au distracteur se trouvent à contrebalancer la présentation visuelle.

Par la suite, nous explorons la composante retrouvé par Dell'Acqua et collègues (2010) lors de la récupération en VSTM. Nous approchons cette composante similaire à la N2pc en supposant qu'il s'agit d'activité liée à la récupération de la cible. Nous utilisons la même technique de séparation de l'activité de la cible et du distracteur utilisée lors du précédent chapitre pour vérifier s'il y a également une activité propre au distracteur. Dans ce cas, le distracteur est un item encodé en mémoire en même temps que la cible dont la tâche ne demande pas la récupération. Au moment de l'encodage de l'information les deux items de

couleur sont des cibles potentielles, car nous ne fournissont la couleur cible qu'au moment de la récupération à l'aide d'un indicateur à la fixation. Ainsi, lors de la récupération, l'information visuelle de la présentation n'est pas latéralisée. La perception de l'indicateur ne produit pas de composante latéralisée. Nous effectuons cette séparation entre cible et distracteur pour vérifier qu'il existe bien des structures corticales latéralisées servant au maintient et à la récupération de l'information en VSTM. Nous désirons également établir des liens entre les mécanismes attentionnels en place durant la perception (N2pc) et l'encodage/rétention (SPCN) et ceux servant à la récupération de l'information visuelle en mémoire.

Enfin, nous vérifions l'impact de distracteurs gris dans une tâche de recherche visuelle « pop-out ». La présence de distracteurs gris ne devrait pas perturber de manière importante une recherche visuelle d'items cibles de couleur. Cependant, des aspects de l'expérience de Hillimire et collègues (2009, 2010) suggèrent la possibilité que des distracteurs gris, forcés par la tâche à être inclus dans le focus attentionnel, ont des effets importants sur le déploiement atttentionnel. Les expériences de Hilimire et collègues (2009, 2010) montrent une plus grande amplitude de la N2pc ainsi qu'une Ptc plus négative pour une distance plus grande entre cible et distracteur saillant. Ces résultats entrent en opposition avec la théorie de la réduction de l'ambiguïté de Luck. Une plus grande distance entre cible et distracteur devrait permettre de réduire l'amplitude de la N2pc selon la TRA. Cela nous fait penser qu'il existe possiblement une explications alternative à leur résultats. En effet, leur tâche donne la possibilité d'utiliser la couleur comme un outil de présélection pour identifier deux cible potentielles, mais exige un recherche attentionnelle plus approfondie pour identifier la cible parmi ces deux items. Ceci pourrait résulter en un focus attentionnel large dicté par la distance qui sépare les deux cibles potentielles. Les distracteurs gris, en nombre croissant avec la distance entre cibles potentielles, seraient alors possiblement responsable de l'ambiguïté croissante au sein du focus attentionnel. Cela aurait pour conséquence, tel de décrit par la TRA, de provoquer une augmentation de la N2pc. Nous avons conçu une tâche qui utilise la couleur pour sélectionner deux cibles potentielles, mais sans changer la distance entre celles-ci l'une par rapport à l'autre.

Ainsi, en ajoutant des distracteur gris, on peut observer leur effet sans qu'il soit confondu avec un effet de distance.

Cette exploration de l'activité attentionnelle electrophysiologique liée aux cibles et aux distracteurs est fondamentale pour la compréhension de l'information que nous pouvons extraire de résultats expérimentaux. L'électrophysiologie est un outil très puissant qui nous permet une mesure objective d'activité autrement invisible avec une grande précision temporelle. Cependant, cette approche repose sur l'interprétation d'information pouvant aisément être confondue. Les interactions attentionnelles entre cibles et distracteurs doivent pouvoir être vérifiées sans équivoque. Au-delà de l'intention expérimentale de voir une cible ou un distracteur, l'action des facteurs ascendants et descendants sur les mécanismes attentionnels peut altérer notre perception et notre mémoire et rendre la distinction entre une cible et un distracteur plus ténue.

Chapitre 1 : The “red-alert” effect in visual search: Evidence from human electrophysiology

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Current views on how task-relevant information is selected from scenes including potentially distracting information agree that two complementary mechanisms operate to achieve this goal. Target information activation is held to be enhanced while distracting information is concomitantly suppressed (e.g., Desimone & Duncan, 1995). Over the past two decades, this synergistic interplay between facilitatory and inhibitory mechanisms has received support from event-related potential (ERP) studies focusing on visual search. These studies have revealed that lateral targets elicit an increase in negativity over the contralateral posterior hemisphere usually unfolding in a 180–280 ms time window, termed N2pc, and usually measured under conditions in which an equivalent distractor is present in the visual hemifield opposite to that occupied by the target (Eimer, 1996; Jolicœur, Brisson, & Robitaille, 2008; Luck & Hillyard, 1994; Robitaille & Jolicœur, 2006; Woodman & Luck, 2003). An elegantly simple experimental design often employed to track processing taking place during target search involves presenting two lateral items, one to the left and one to the right of fixation, and monitoring the amplitude and latency of the N2pc response as a function of a variety of experimental manipulations (e.g., Dell’Acqua, Sessa, Jolicœur, & Robitaille, 2006; Eimer, 1996; Jolicœur, Sessa, Dell’Acqua, & Robitaille, 2006a, 2006b). One limitation of this approach is that it is difficult to distinguish activity related to processing of the target and distractor(s) in the ensuing N2pc. The N2pc waveform is calculated by subtracting from the activity measured on the scalp at contralateral electrode sites relative to the target the activity measured at corresponding ipsilateral electrode sites, thus potentially conflating brain activity

elicited by all lateral items (i.e., target on one side and distractor on the other) in the visual search display into a single component.

In an elegant inversion of the logic of examining lateralized brain activity in response to lateral stimuli, Woodman and Luck (2003) isolated activity of a lateral stimulus from another salient stimulus by presenting this latter item on the vertical meridian. The item on the vertical meridian is both in the left and the right visual hemifield, and so it cannot produce a systematic brain lateralization as a function of the position of another lateral item presented sometimes in the left and sometimes in the right visual field, thereby nullifying any systematic lateralization of brain activity of the item on the vertical meridian. Hickey, Di Lollo, and McDonald (2009) used the method introduced by Woodman and Luck (2003) in search displays in which one stimulus was a lateral item and one was placed eccentrically along the vertical meridian. When the lateral item was a target, event-related lateralizations (ERLs) showed a component similar to the N2pc, which they named N_T (negativity related to the target). When the lateral item was a distractor, the ERLs showed a positivity between 230 ms and 280 ms after the presentation of the search display, contralateral to the lateral distractor, which was termed P_D (positivity related to the distractor). They hypothesized that the P_D component reflected a process of distractor suppression. Sawaki and Luck (2010) also found a positivity related to a distractor, but in a much earlier time window, namely between 115 ms and 225 ms. The difference in timing beween Hickey's and Sawaki's distractor-induced positive reactions could perhaps be explained by differences in the experimental paradigms, but could also reflect a different process altogether. Whereas Hickey et al.'s (2009) arguments were based on a distractor that was always a red line that had been adjusted to match the subjective brightness of the background, Sawaki and Luck (2010) used displays containing a salient uniquely colored lateral distractor, either green or red. The latency of the P_D as well as the experimental condition in the Sawaki and Luck (2010) experiments would tend to suggest the component is a positive posterior contralateral component (Ppc), which has been linked to a sensory imbalance in the physical structure of search displays (Corriveau et al., 2012; Fortier-Gauthier, Moffat, Dell'Acqua, McDonald, & Jolicœur, 2012; Leblanc, Prime, &

Jolicœur, 2008). The salience and color differences between Hickey's and Sawaki's experimental paradigms could have caused the differences observed across experiments in terms of contralateral positive deflections.

On the other hand, while examining the potential causes of this temporal discrepancy between the two mentioned studies, we noted that a systematic ERP investigation of the role of color in modulating lateralized ERP responses in visual search, at least to our knowledge, has never been conducted as of yet. Color is well known as a privileged feature facilitating the attentional processing of a visual stimuli (Wolfe, 2000; Wright, 1972), and there is a vast psychophysical and visual search literature, but reports of chromatic attentional effects (color-to-color) in other paradigms and on lateralized ERP components are scarce. A flanker task experiment (McCarley & Mounts, 2008) raised the question that color-specific bias, for equiluminant colors, could play a role in attentional processing when they showed a stronger interference in a green-red target-flanker pair when the flanker was red. Exploring whether a class of attention-modulated ERP responses in visual search are bound to the choice of specific colors (or differences in color between targets and distractors) is of obvious importance, as it may lead to revisit claims on the functional characterization of ERP (sub)components in the N2 range that largely prescinded, in their original formulations, considerations of this physical dimension.

Examining the electrophysiological manifestations of attentional control, selection of targets, and suppression of distractors, while also examining the potential impact of specific colors chosen for target/distractor is the aim of the present investigation. As done by Hickey et al. (2009), we placed one colored item (e.g., red) on the vertical meridian and one item of a different color (e.g., green) in a lateral position, in a display otherwise composed of gray distractors, as illustrated in Figure 1. All of these stimuli had the same luminance, which equated the overall luminance afferent stimulation from each visual hemifield. Luminance was equated using a Minolta CS100 chromameter. We found, in concurrent work, that the

adjustments based on this instrument match those found by psychophysical adjustments based on heterochromatic flicker photometry (Shioiri & Cavanagh, 1992). As shown in Figure 1, all of our stimuli were more luminous than the background, and the luminance adjustments of the red, green, and gray stimuli ensured that the sensory inputs from the two hemifields were approximately equal. We note that the procedure used by Hickey et al. (2009) was different. They asked participants to adjust the subjective brightness of a red stimulus to match the brightness of the background (both low intensity), and they also used a much brighter green stimulus. They dealt with associated afferent differences between hemifields by experimentally manipulating which stimuli were to be attended or ignored via task relevance, which was a reasonable approach. We prefer to equate luminance rather than subjective brightness because luminance is closely linked to underlying neurophysiological channels in the visual system, which we are trying to equate across visual fields, and correlates better with achromatic form perception than brightness (Shioiri & Cavanagh, 1992).

Experiment 1

Method.

Participants.

Twenty-five participants completed Experiment 1 voluntarily and received monetary compensation in an experiment vetted by the Ethics Committee of the Faculty of Arts and Science at Université de Montréal. They had normal or corrected-to-normal vision, were neurologically normal, and were not taking neurologically active medication according to self-reports. Data from 20 were kept for analysis (15 women) with a mean age of 23.1 (19 to 30 years old). Among the rejected participants, four were rejected due to excessive eye blinks and eye movements toward a lateral item, and one participant was rejected due to near-chance accuracy (criterion described in the Recordings section).

Stimuli.

An example of the stimuli and trial design in Experiment 1 are illustrated in Figure 1.

<<< INSERT FIGURE 1 HERE >>>

Two types of displays were used. The cue display was a single colored circle around the gray fixation dot indicating the target color for the current trial. The search display consisted of 10 nearly equiluminant circles (red: 11.1 ± 0.1 cd/m^2 , x = .629, y = .345; green: 11.2 ± 0.1 cd/m^2 , x = .303, y = .591; gray: 10.9 ± 0.1 cd/m^2 , x = .264, y = .312) evenly distributed along an imaginary circle (8° of diameter) centered at fixation. Each circle had a diameter of 1.5° of visual angle. The uppermost and lowermost circles were on the vertical meridian, and two circles were positioned in each quadrant, with no circle on the horizontal meridian. Each circle contained a line with a length of 0.9° of visual angle at one of four possible orientations (horizontal, vertical, 45° tilted to the left oblique, or 45° tilted to the right). All circles were gray with the exception of two circles, one red and one green. The positions of the red and green circles were varied from trial to trial, but in each display one colored circle was in one of the two vertical meridian positions while the other was lateral. The lateral colored circle was always at a distance of 3 positions (2 intercalated items) from the vertical meridian colored circle. The stimuli were presented in a dimly lit room on a Viewsonic P75f+ cathodic monitor.

Design and procedure.

Each trial started with the presentation of a fixation point. The fixation point remained visible throughout the trial until a feedback was presented at the end of the trial. A 400-ms color-cue display was presented 400–600 ms after the space bar press. The target/distractor color mapping was determined at run time, and with equal probability. A 1,000-ms blank interval followed the offset of the color-cue display. The search display then appeared until a response was detected, or 3,000 ms had elapsed. The participant had to indicate, as quickly and accurately as possible, the orientation of the bar inside the target-color circle (i.e., the circle of the same color as the color-cue), disregarding all other items in the search display, by pressing one of four response keys. Response hand was counterbalanced across participants.

Participants instructed to use their left hand used the {x, c, v, b} keys, whereas participants instructed to use their right hand used the {n, m, , (comma), . (period)} keys on a North American QWERTY keyboard, each key corresponding to one line orientation {tilted to the left, vertical, horizontal, tilted to the right, respectively}. Feedback on response accuracy was shown at fixation (+ or - signs) at the end of the trial for 500 ms. Participants completed 1 block of 32 practice trials followed by 8 blocks of 128 experimental trials.

EEG recordings and analysis.

The electroencephalogram (EEG) was recorded with 64 active scalp Ag/AgCl electrodes (BioSemi ActiveTwo system) mounted on an elastic cap. Positioning and naming of the electrodes followed the International 10-10 system (Sharbrough et al., 1991). Data were digitized at a sampling rate of 256 Hz, low-pass filtered online at 67 Hz, and band-pass filtered offline between 0.05 and 20 Hz in postrecording analyses. Trials with a correct response were segmented, time-locked to the onset of the search display, from 200 ms prior to display onset to 600 ms after (800 ms total). These segments were averaged and baseline corrected based on the mean activity during the 200-ms prestimulus period. The horizontal electrooculogram (HEOG) was recorded and computed as the difference between signals at two additional electrodes located on the external canthi of each eye. The vertical electrooculogram (VEOG) was recorded and computed as the difference between signals at an electrode located above (FP1) and an additional electrode below the left eye. Two additional electrodes were used to record signals at the left and right mastoids, and all signals were rereferenced in postrecording analysis to the average of the voltage at the mastoids. Trials with blinks were rejected based on VEOG variations of more than 50 μV in a 200-ms time window scrolled throughout each trial segment duration. Trials with horizontal eye movements, defined as HEOG variations larger than 40 μV in a 200-ms time window scrolled through each trial segment, were rejected. We rejected data from participants who had less than 50% of trials retained after removing incorrect responses and trials with blinks or eye movements when trials were split across experimental conditions.

Component amplitude measures for statistical analysis were obtained by averaging the time-point measurements over a time period surrounding a period of interest for each electrode. This period of interest was centered on the time of peak amplitude for the grand-averaged waveform across participants, for a particular component. When no discernible component could be seen, the time of peak amplitude from a corresponding condition was used instead. The width of the averaging period was set to 50 ms for the N2pc, and 30 ms for the shorter Ppc and P_D components. The latency statistics on the N2pc were evaluated using the jackknife technique. The jackknife method is based on the computation of N jackknife grand averages where each average is based on N-1 participants, removing each participant from one of the averages. The latency at which the N2pc in each of these jackknife grand-averaged waveforms reached an amplitude of -1 μV was measured and submitted to an analysis of variance (ANOVA) corrected by dividing the calculated F by $(N-1)^2$ to correct for the reduced error variance of estimated values (Kiesel, Miller, Jolicœur, & Brisson, 2008; Ulrich & Miller, 2001).

Results.

Behavior.

The mean response time (RT) for red targets was shorter than for green target trials (RT_R = 783 ms, σ = 137.24; RT_G = 801 ms, σ = 132.28; F(1,19) = 7.00, p < .016). Mean accuracy for red targets was not significantly different from accuracy for green targets (Acc_{RED} = 91%, σ = .06; Acc_{GREEN} = 92%, σ = .06, F(1,19) = .45; p > .51).

ERP/ERL.

Using our current paradigm, we expected to see a P_D at a slightly longer latency compared to the N2pc only in the trials where the distractor was lateral. Hickey et al. (2009)

reported a P_D timing of about 230–280 ms. The lateral distractor trials ERLs, shown in Figure 2, revealed a more complex picture. When a red circle was the lateral distractor, two positive components appeared in the ERL waveforms, one preceding and one following the N2pc, peaking respectively at 142 ms and 296 ms. Based on the results and arguments of Hickey et al. (2009), we associated the second positivity as likely equivalent to the P_D, whereas the first component would be akin to the Ppc or to the P_D found by Sawaki and Luck (2010). On the other hand, when the lateral distractor was green there was no significant component visible. The t tests against zero for each component are reported in Table 1 for all conditions.

<<< INSERT FIGURE 2 HERE >>>

When we examined results for trials with a lateral target (Figure 2), we found the typical N2pc for a lateral red or green target. However, the N2pc was delayed for the lateral green target trials compared to the lateral red target trials (mean onset latency, M_{RED} = 174 ms, σ = 1.26; M_{GREEN} = 210 ms, σ = 1.48; $F_{CORRECTED}$ (1,19) = 64.5; $p < .0001$). A Ppc was present for the red and the green targets. An ANOVA with factors color (red vs. Green) and status (target vs. distractor) for each component (N2pc, Ppc, and P_D) revealed (see Table 2) a color main effect for each component as well as a status main effect for the N2pc. The three components had larger amplitudes for red circles compared to green circles, regardless of their status as target or distractor. The Ppc and the P_D nearly reached significance for an interaction Color X Status, which tended to be supported by the t test against zero patterns from Table 1. The Ppc failed to reach significance when the distractor was green, whereas the P_D only reached significance for a red distractor.

<<< INSERT TABLE 1 HERE >>>

The differences between the red and green waveforms encouraged us to look for distractor-related positivity for each color separately. As can be seen in Figure 2, when the target was red we observed the same positivity before and after the N2pc as when the lateral circle was a red distractor. When the target was green, we only saw a Ppc (before the N2pc) and there was no P_D, while there was neither a Ppc nor a P_D when the lateral distractor was green.

Discussion.

The delayed N2pc latency for a green target compared to a red target combined with longer RTs for green targets compared to red targets suggests a processing difference between red and green that begins at least as early as the N2pc time range. The presence in red distractor trial ERLs of a component such as a Ppc, which is present in red lateral target trials but absent from green lateral distractor trial ERLs, also supports such an interpretation. The red circles show signs of preferential attentional treatment even though their luminance was the same as for the gray and green circles.

These results seem at odds with the suggestion of Hickey et al. (2009) that the P_D would be related to processes of distractor suppression. The red distractor ERLs show waveforms (Figure 2) similar to the red targets, which should supposedly only show a positive component in the 230 ms to 280 ms time range. On the other hand, green distractor ERLs do not show (Figure 2) any indication of attentional treatment of the lateral item. In addition, the green distractor circle failed to produce any actual status effect between target and distractor for the Ppc as well as the P_D. We surmise that the difference in positivity following the N2pc as a function of the color of the lateral stimulus reflects a substantial processing imbalance between these particular colors. We note that this difference was not controlled in the Hickey et al. (2009) experiment because their lateral item for critical conditions was always red.

Although the post-N2pc contralateral positivity was not strongly modulated by the target versus distractor distinction, N2pc was very strongly modulated. A large N2pc was observed only when the lateral item was a target, whether this item was red or green.

Experiment 2

The results of Experiment 1 show that the N2pc should not always be interpreted as the sum of a negativity contralateral to the target (reflecting target selection) and a positivity contralateral to the distractor (reflecting distractor suppression). The marginally significant N2pc for the red distractor trials, combined with its absence in green distractor trials, may indicate that a processing difference across colors led to a partial loss of control during attentional deployment. The simplest explanation would be that during a subset of trials participants deployed their attention to the red distractor first instead of the green target. An alternate explanation would be that the distractor processing during the N2pc time range is proportional to an attentional priority difference between the distractor and the target (here as a function of color).

However, we may wonder if the absence of specific distractor-related activity may have resulted from the random selection of target color (and hence of the distractor color) on each trial. The frequently changing color of the distractor may have prevented the formation of a more stable endogenous bias against a specific distractor color. Woodman, Luck, and Schnall (2007) found, for example, that there was more dual-task interference on visual search by a concurrent requirement to hold information in visual short-term memory when a target defined by shape changed from trial to trial than when the target shape was kept constant during trial blocks. This suggests that holding the selection criteria for the target constant may facilitate the use of a processing strategy that makes visual search less subject to interference from concurrent distractors (perhaps because of a processing of distractor inhibition that is sensitive to concurrent load). In Experiment 2, we tested this possibility by holding the target and distractor color constant throughout each block of trials. We hypothesized that blocking the trials by target/distractor color would enable a stronger top-down control over distractor inhibition, as well as over target selection. Such a greater top-down influence could overcome (in part or in whole) the apparent color imbalance between the green and the red stimuli that was evident in Experiment 1.

Method.

Participants.

Participants completed the experiment voluntarily and received monetary compensation. They had normal or corrected-to-normal vision, were neurologically normal, and were not taking neurologically active medication. From the 27 participants who completed Experiment 2, 21 were kept for analysis (10 women) with a mean age of 22.2 (19 to 28 years old). The excluded participants were rejected due to excessive numbers of ocular artifacts (blinks and ocular movements toward the lateral singleton). All participants signed an informed consent in accordance with the Université de Montréal Faculty of Arts and Science Ethics Committee guidelines.

Stimuli, design, and procedure.

Stimuli and task were the same as in Experiment 1, except that instead of specifying the target color at random trial by trial, we alternated the target color (and hence the distractor color) block by block, balancing the order of presentation across participants. As in Experiment 1, there were 8 blocks of 128 trials.

Results.

Behavior.

As in Experiment 1, the mean RT was shorter for red targets than for green targets (RT_{RED} = 739 ms, σ = 85.2; RT_{GREEN} = 759 ms, σ = 83.08; $F(1,20) = 8.73$; $p < .008$). The mean accuracy (percent) did not differ across target color (Acc_{RED} = 95.8%, σ = .02; Acc_{GREEN} = 95.4%, σ = .03; $F(1,20) = 1.31$; $p > .26$).

ERP/ERL.

As reported in Table 1, the results revealed essentially the same general ERL components in Experiment 2 as in Experiment 1. The most important findings, based on the ERLs for lateral distractors and targets, for each color are shown in Figure 3. When the lateral distractor was red, we observed a Ppc and a P_D, but when the lateral distractor was green, we found only a Ppc, which although visible in the waveform in Experiment 1 did not reach statistical significance in that experiment. When the lateral target was red or green, we observed a Ppc followed by an N2pc. The N2pc was delayed for the lateral green targets compared to the lateral red targets (M_{RED} = 203 ms, σ = 1.55; M_{GREEN} = 229 ms, σ = 1.03; $F(1,20) = 24.9$; $p < .0001$). An ANOVA with factors color (red vs. green) and status (target vs. distractor) comparing each component amplitude (N2pc, Ppc, and P_D) revealed (see Table 2) an expected N2pc status (target vs. distractor) main effect and a Color X Status interaction for the P_D. The P_D was significantly larger, and significantly different from zero, for a lateral red distractor than for the other conditions. A color amplitude effect was not found for the Ppc or the N2pc.

<<< INSERT FIGURE 3 HERE >>>

<<< INSERT TABLE 2 HERE >>>

In order to compare results across experiments, we performed additional analyses by including experiment as a between-subjects factor in ANOVAs that were otherwise like those used for each experiment. The most important results are summarized in Table 3. We found an interaction between experiment and target-distractor status in which only the lateral targets elicit an N2pc, and the amplitude was larger for mixed trials (Experiment 1) than for blocked trials (Experiment 2) for the N2pc component only. This is a very interesting result because it demonstrates a modulation of the N2pc despite the use of identical stimuli (target, distractor, and fillers), based on whether the target-distractor relationship changed frequently or infrequently. Importantly, this modulation was substantial for both red and green lateral targets and suggests that the N2pc might reflect a greater effort at early stages of processing in order to compensate for a less well-established top-down selection filter. There was also an

interaction between color and experiment for the N2pc reflecting a change in the relative amplitude of the N2pc for red and green targets across the experiments. Our interpretation of this result is somewhat speculative, but consistent with the results of Woodman et al. (2007). The changing color assignment from trial to trial in Experiment 1 may have made it more difficult to maintain an effective selection filter for green targets, allowing more bottom-up color differences to influence the results. This would give a greater relative advantage to red in Experiment 1 than in Experiment 2. More work will be needed to verify this speculative hypothesis. We also found a near significant interaction of experiment and color for the Ppc and the P_D, raising some possibility of a real difference for these components between the two experiments. Averaging across experiments, we found a color main effect, with larger Ppc and P_D amplitudes for red than for green. The P_D color main effect was overshadowed by an interaction of status and color reflecting a larger P_D for lateral red distractors followed by a lateral red target, which is not significantly different from 0, $t(40) = 1.49$; $p > .14$, supporting the proposal that the amplitude, if not the presence, of the P_D was driven by the fact that the lateral item was red.

<<< INSERT TABLE 3 HERE >>>

Discussion.

As in Experiment 1, the N2pc in Experiment 2 was earlier for red targets than for green targets. However, unlike what we found in Experiment 1, there was no amplitude difference across red and green targets. It is likely that participants were able to prepare better when target and distractor colors were constant for entire blocks of trials. Although blocking target and distractor colors reduced the color-related imbalance on N2pc amplitude, it did not remove the latency advantage for red over green also found in Experiment 1. These results are important because they suggest that, despite the use of equiluminant stimuli, there can be systematic differences in the speed with which attention can be deployed to targets selected on the basis of different colors. The latency difference across red and green targets suggests that red has a higher overall attentional priority than green, at least in the present context.

Not only were target-related processes affected by blocking color, but so were those engaged by the distractors. For example, we observed a Ppc for the lateral green distractors in Experiment 2 that was not evident in Experiment 1 (not blocked). The Ppc might function as an "attend-to-me" signal caused by an imbalance in the physical properties of the display. However, the fact that the Ppc was not observed when the distractor color changed randomly from trial to trial (Experiment 1), but was found when the distractor color was constant during whole trial blocks (Experiment 2) suggests that the Ppc may be partially driven by endogenous factors. Sawaki and Luck (2010) were able to make the Ppc disappear by forcing the attention away from the imbalanced element in the display with a difficult task for stimuli at the fixation. Interestingly, here we had the same task and exactly the same physical display across different experiments. The only difference across experiments was whether the role of particular colors varied frequently (across trials) or infrequently (across blocks). If the Ppc reflected only purely exogenous stimulus factors, we should have observed equivalent Ppccomponents in the two experiments for both colors. The Ppc was, in fact, quite similar across experiments for red distractors, perhaps because processing for red was more strongly influenced by bottom-up factors. The contextual change induced by mixing versus blocking target and distractor color status had a stronger effect for processing green stimuli, perhaps because green was inherently less salient based on bottom-up signals. The weaker bottom-up influence may have allowed top-down influences to be more easily observed. The blocking of distractor color may have given the lateral green distractor a special status that increased the attentional priority for green, resulting in a significant Ppc in the blocked trials of Experiment 2, perhaps using the same mechanisms as in the paradigm of Woodman et al. (2007). Experiment 2 still showed significant color imbalances that make it difficult to isolate a distractor-specific ERL. The pattern of activation for the lateral red and green distractors both show a Ppc (Figure 3), but only red distractors have a P_D. The presence of the P_D for red distractors is tantalizing as potential evidence for a mechanism of distractor suppression given the apparent absence of the component for red targets. One possibility is that the N2pc, which is a strong contralateral negativity, overrides the positivity that might have been visible in the absence of target-specific processing leading to the N2pc on lateral red target trials. Perhaps the most important finding here, therefore, was the complete absence of a P_D for green distractors, despite blocking distractor color, and clear evidence for a Ppc and N2pc for green

targets and a Ppc for green distractors. In short, the pattern of results provides, at best, equivocal evidence for a process of distractor suppression expressed in a contralateral P_D. We note that the Hickey et al. (2009) experiments all had a red lateral distractor (with subjective brightness matched to the background) and trials were blocked. This is not to say that the Hickey et al. (2009) results did not reflect distractor suppression. It is entirely possible that the significantly different experimental conditions in their experiments made it possible to observe such a mechanism. Three things are clear from our results. Firstly, lateral distractors do not invariably produce a clear P_D component. Secondly, the specific colors used in search experiments can have significant influences on patterns of event-related potentials, including lateralized potentials important in the study of visual- spatial attention. And thirdly, the necessary and sufficient conditions needed to observe distractor suppression expressed in a P_D component are not known at this time. More research is needed to delimit the boundary conditions for this potentially very interesting component.

General Discussion

The N2pc latency difference in both experiments and the amplitude effect of color in Experiment 1 for the Ppc, N2pc, and P_D indicate a clear processing imbalance across red and green, despite equiluminance, which is usually not considered explicitly in most attention experiments. The calculation of the N2pc combines effects from lateral targets and distractors and typically averages over color effects when stimuli are carefully counterbalanced across all conditions. However, this approach may hide interesting systematic differences across stimuli. Such effects were revealed in the present investigation. In both experiments, the red-green color difference dominated the differences between target and distractor for the Ppc and the P_D, and had a very noticeable latency effect for the N2pc. The blocking of the target color seemed to be sufficient to reduce the amplitude effect of color on the Ppc and N2pc components, but the latency effect remained for the N2pc. This reduction of the color imbalance is possibly explained by the adoption of top-down selection and rejection filters, based on the stable relationship between color and target versus distractor status, when trials are blocked (Woodman et al., 2007). This may have enabled participants to be less strongly

influenced by purely bottom-up factors. The Ppc and the P_D appear to be more strongly related to exogenous, physical properties of the items than to endogenous status imposed by the task. Given the frequent use of red and green as colors in attention experiments, the present results suggest that experimenters should be cautious in how experiments are designed and how results are interpreted. For example, in the work of Hickey et al. (2009), one might wonder to what extent the observed contralateral positivity associated to distractors was due to the consistent use of a red lateral stimulus as distractor, as opposed to a process of distractor suppression. It is possible that the use of a color stimulus matched in brightness with the background, and not balanced by a corresponding stimulus in the opposite hemifield as in the Hickey et al. (2009) paradigm, would reveal a contralateral positivity to green distractors. Such an experiment would be a useful extension and confirmation of the Hickey et al. (2009) interpretation of the P_D.

In the present preparation, we did not observe a contralateral positivity, in either experiment, when the lateral distractor was green (and the midline target was red). Hickey et al. (2009) proposed that the P_D may indicate an inhibition process observable when a distractor is presented laterally, even if the distractor is not overly strong (red line with a similar brightness as the background). It is possible that a green target was such a weak distractor, in the presence of a red target, that a specific active process of distractor suppression was not engaged. However, we remain cautious regarding the existence and meaning of the P_D. The present results suggest that to observe the P_D component requires specific conditions, and those conditions were not met by our experiment. A useful test of the functional interpretation of the contralateral positivity (P_D) often, but not always, found after the N2pc, would be to repeat experiments such as the present Experiment 2, but with colors chosen to be more equally prioritized, from the point of view of attentional mechanisms. Equal attentional priority could be operationalized as an N2pc of equal amplitude and latency or the absence of a Ppc before the N2pc for lateral targets in those colors.

The present results provide interesting evidence suggesting that the Ppc, the positivity posterior and contralateral observed prior to the N2pc, is not only a reflection of sensory differences across the stimuli. Had this been the case, the Ppc for green lateral distractors should have been the same in the two experiments. Blocking or mixing the role of green as a target or distractor color modulated the amplitude of the Ppc, suggesting therefore that the Ppc is sensitive to experimental context, and thus not simply a reflection of bottom-up sensory differences.

Finally, the results suggest that red stimuli may enjoy a special status in the context of visual search designs like the ones employed in the present work, and in many other similar experiments in the literature (e.g., Hickey et al., 2009; Hillimire, Mounts, Parks, & Corballis, 2009; Mazza, Turatto, & Caramazza, 2009). This possible special status of red occurs despite balancing stimuli for luminance and suggests that further work on the color differences found here would be clearly warranted given the relative impact of this factor. Of course, the present results are quite limited because they examined only a particular red and green color, and as such they invite a broader investigation involving more colors. Our goal was not to offer a definitive solution to the issue, but rather sound an alarm. At the very least, the present work should serve as a red alert to all researchers, but particularly to researchers using sensitive electrophysiological methods, to pay close attention to the specific colors used in studies designed to elicit visual event-related responses, and to how they impact the results.

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Figure captions

Figure 1. Timecourse of Experiment 1 and 2 display presentations. The lateral colored item can be either a target or distractor and the target color was displayed in the cue presented around the fixation point early in the trial. In Experiment 2, the target color was blocked so the cue presented before the search display was the same during a block, whereas in Experiment 1 it changed pseudo-randomly trial by trial.

Figure 2. Results from Experiment 1. Grand average contralateral minus ipsilateral waveforms, at electrode pair PO7–PO8, for the lateral color singleton, for each Color (red vs. green) and Status (target vs. distractor). The curves are generally characterized by an early positivity posterior and contralateral (Ppc), followed by an N2pc, and a subsequent P_D. See text for further details.

Figure 3. Results from experiment 2. Grand average contralateral minus ipsilateral waveforms, at electrode pair PO7–PO8, for the lateral color singleton, for each Color (red vs. green) and Status (target vs. distractor). The latency difference between the red and green N2pc is still present while blocking target color. The curves are generally characterized by an early positivity posterior and contralateral (Ppc), followed by an N2pc, and a subsequent P_D. See text for further details.

Figure 1

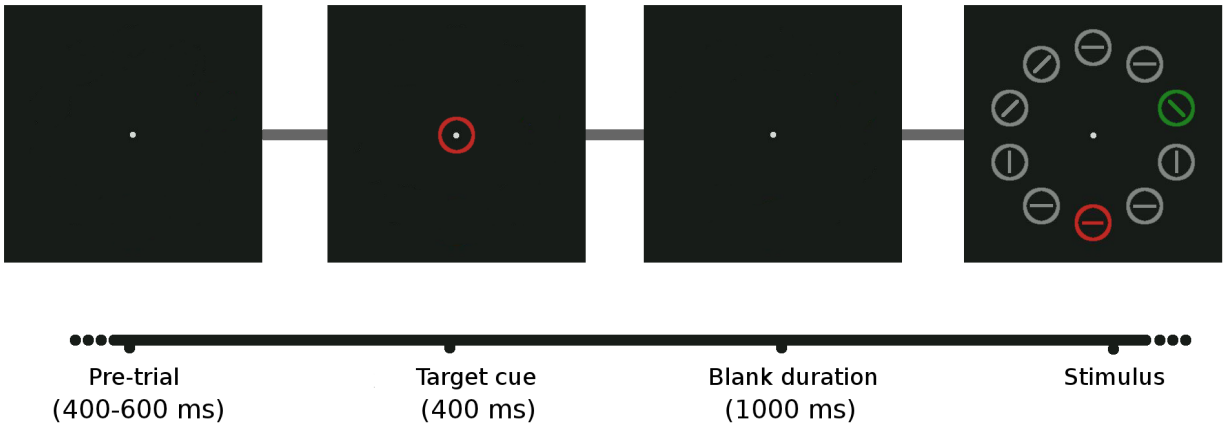
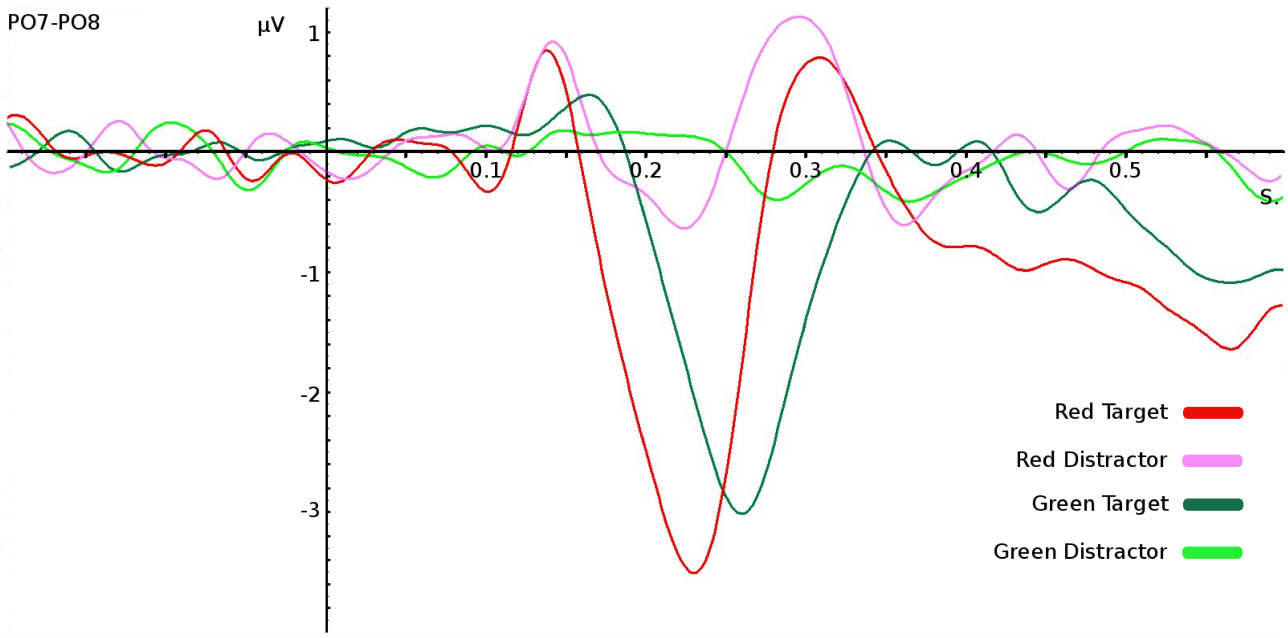

Pre-trial
(400-600 ms)
Target cue
(400 ms)
Blank duration
(1000 ms)
Stimulus

Figure 2


PO7-PO8
µV
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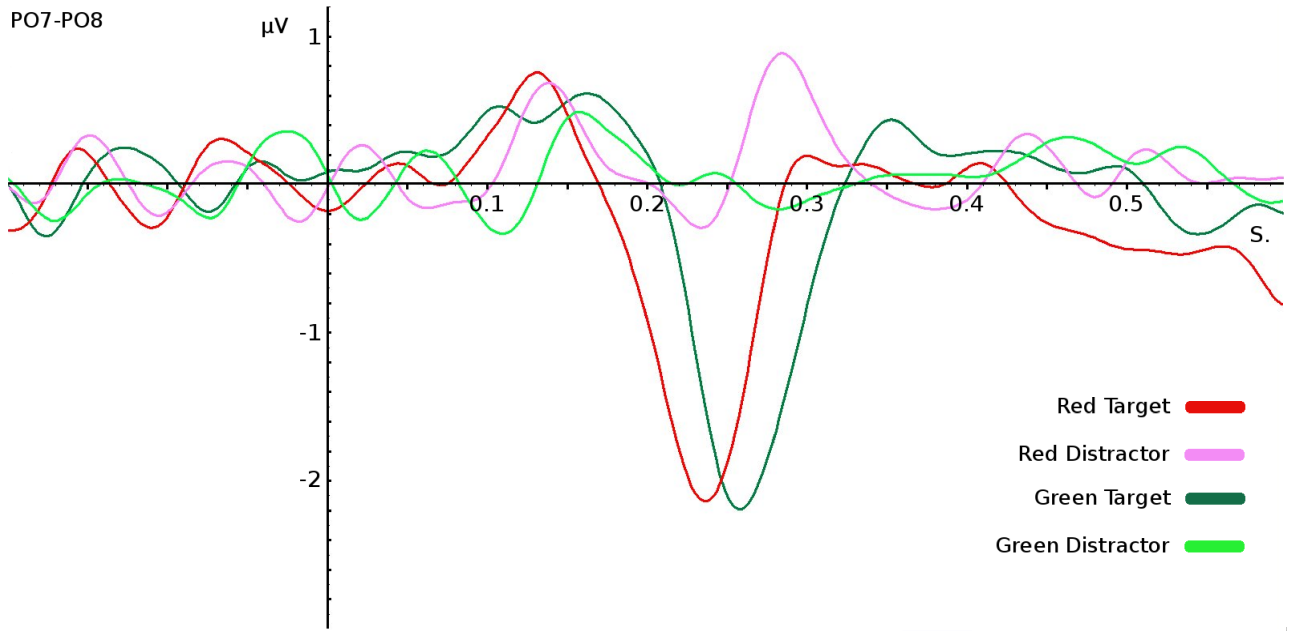
Red Target
Red Distractor
Green Target
Green Distractor

Figure 3


PO7-PO8
µV
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S.
Red Target
Red Distractor
Green Target
Green Distractor

Tables

Table 1. Time range (ms), average amplitude (µV) and *t*-test against 0 of each component for each Color and Status condition of both experiments.

Exp.	Color	Status	N2pc	Ppc	P_D
1	Red	Target	205ms - 255ms	123ms - 153ms	295ms - 325ms
			M=-3.149µV; σ=2.2	M=.669µV; σ=.99	M=.731µV; σ=2.05
			t(19)=6.399;	*t*(19)=3.035;	*t*(19)=1.596;
			p < .00001 *	*p* < .007 *	*p* < .127
		Distractor	199ms - 249ms	127ms - 157ms	281ms - 311ms
			M=-.471µV; σ=1.07	M=.784µV; σ=.62	M=1.089µV; σ=1.39
			t(19)=1.967;	*t*(19)=5.651;	*t*(19)=3.502;
			p < .064	*p* < .00002 *	*p* < .002 *
	Green	Target	234ms - 284ms	148ms - 178ms	338ms - 368ms
			M=-2.714µV; σ=1.96	M=.428µV; σ=.73	M=.047µV; σ=1.72
			t(19)=6.186;	*t*(19)=2.627;	*t*(19)=.123;
			p < .00001*	*p* < .017 *	*p* < .903
		Distractor	199ms - 249ms	127ms - 157ms	281ms - 311ms
			M=.124µV; σ=.67	M=.122µV; σ=.72	M=-.31µV; σ=.9
			t(19)=.826;	*t*(19)=.761;	*t*(19)=1.536;
			p < .419	*p* < .456	*p* < .141
2	Red	Target	211ms - 261ms	115ms - 145ms	285ms - 315ms
			M=-1.864µV; σ=1.18	M=.686µV; σ=.96	M=.131µV; σ=1.58
			t(20)=7.256;	*t*(20)=3.274;	*t*(20)=.381;
			p < .000001 *	*p* < .004 *	*p* < .707
		Distractor	209ms - 259ms	123ms - 153ms	269ms - 299ms
			M=-.155µV; σ=.92	M=.617µV; σ=.63	M=.799µV; σ=.93
			t(20)=.778;	*t*(20)=4.513;	*t*(20)=3.952;
			p < .446	*p* < .0003 *	*p* < .0008 *
	Green	Target	234ms - 284ms	148ms - 178ms	338ms - 368ms
			M=-1.915µV; σ=1.4	M=.584µV; σ=.9	M=.387µV; σ=2.01
			t(20)=6.282;	*t*(20)=2.957;	*t*(20)=.881;
			p < .00001 *	*p* < .008 *	*p* < .389
		Distractor	257ms - 307ms	142ms - 172ms	342ms - 372ms
			M=-.121µV; σ=.69	M=.433µV; σ=.54	M=.061µV; σ=.92
			t(20)=.798;	*t*(20)=3.682;	*t*(20)=.306;
			p < .434	*p* < .001 *	*p* < .763

* statistically significant at a p < .05 level.

Table 2. Average amplitude (μV) and ANOVA F values of each component for factors Color and Status for both experiments.

Exp.	Component	Contrast		
		Color	Status	Color X Status
1	N2pc	M_R=-1.81μV σ=2.18 M_G=-1.3μV σ=2.04 $F(1, 19)$=4.91 $p < .039$ *	M_T=-2.93μV σ=2.07 M_D=-.17μV σ=.93 $F(1, 19)$=49.18 $p < .000001$ *	$F(1, 19)$=.33 $p < .57$
	Ppc	M_R=.73μV σ=.82 M_G=.28μV σ=.73 $F(1, 19)$=11.77 $p < .003$ *	$F(1, 19)$=.31 $p < .585$	$F(1, 19)$=3.4 $p < .081$
	P_D	M_R=.91μV σ=1.74 M_G=-.13μV σ=1.37 $F(1, 19)$=11.68 $p < .003$ *	$F(1, 19)$=.00 $p < .999$	$F(1, 19)$=3.22 $p < .089$
2	N2pc	$F(1, 20)$=.01 $p < .943$	M_T=-1.89μV σ=1.28 M_D=-.14μV σ=.8 $F(1, 20)$=32.88 $p < .00001$ *	$F(1, 20)$=.07 $p < .801$
	Ppc	$F(1, 20)$=1.88 $p < .186$	$F(1, 20)$=.34 $p < .566$	$F(1, 20)$=.06 $p < .804$
	P_D	$F(1, 20)$=.79 $p < .383$	$F(1, 20)$=.27 $p < .606$	M_{TR}=1.89μV σ=1.28 M_{DR}=.13μV σ=1.58 M_{TG}=.06μV σ=.92 M_{DG}=.8μV σ=.93 $F(1, 20)$=4.43 $p < .048$ *

* statistically significant at a p < .05 level.

Table 3. Average amplitude (μV) and ANOVA F values of each component for factors Experiment, Color and Status.

Contrast	N2pc	Ppc	P_D
Experiment	$F(1, 39)=3.18$ $p < .082$	$F(1, 39)=.24$ $p < .625$	$F(1, 39)=.02$ $p < .886$
Status	M_T=-2.4μV σ=1.78 M_D=-.16μV σ=.86 $F(1, 39)=82.08$ $p < .00000001$ *	$F(1, 39)=.65$ $p < .426$	$F(1, 39)=.13$ $p < .723$
Color	$F(1, 39)=3.78$ $p < .059$	M_R=.69μV σ=.8 M_G=.39μV σ=.74 $F(1, 39)=12.34$ $p < .001$ *	M_R=.68μV σ=1.55 M_G=.05μV σ=1.47 $F(1, 39)=9.67$ $p < .004$ *
Experiment X Status	M_{T1}=-2.93μV σ=2.07 M_{D1}=-.17μV σ=.93 M_{T2}=-1.89μV σ=1.28 M_{D2}=-.14μV σ=.8 $F(1, 39)=4.14$ $p < .049$ *	$F(1, 39)=.00$ $p < .956$	$F(1, 39)=.12$ $p < .731$
Experiment X Color	M_{R1}=-1.81μV σ=2.18 M_{G1}=-1.3μV σ=2.04 M_{R2}=-1.01μV σ=1.35 M_{G2}=-1.02μV σ=1.42 $F(1, 39)=4.23$ $p < .046$ *	$F(1, 39)=3.41$ $p < .072$	$F(1, 39)=3.88$ $p < .056$
Status X Color	$F(1, 39)=.31$ $p < .58$	$F(1, 39)=1.52$ $p < .225$	M_{TR}=.42μV σ=1.82 M_{DR}=.94μV σ=1.17 M_{TG}=.22μV σ=1.86 M_{DG}=-.12μV σ=.92 $F(1, 39)=7.64$ $p < .009$ *
Experiment X Status X Color	$F(1, 39)=.03$ $p < .865$	$F(1, 39)=.71$ $p < .403$	$F(1, 39)=.2$ $p < .656$

* statistically significant at a $p < .05$ level.

Chapitre 2 : Contralateral cortical organisation of information in visual short-term memory: Evidence from lateralized brain activity during retrieval

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Visual short-term memory (VSTM) is an important fundamental mechanism in the human cognitive architecture. By establishing a bridge between early sensory input to various cognitive operations, VSTM performs an essential temporary maintenance function that enables the integration of multiple or complex visual input, and is thus critical in many everyday activities. Recent work provides some evidence concerning the cortical networks implicated during the retention of visual information in VSTM (e.g., Grimault et al., 2009; Robitaille et al., 2010; Todd & Marois, 2004). Much of this evidence has focused on manipulations of memory load and examined brain activity during the retention interval. These studies are based on the assumption that brain regions mediating the retention of information will be more active when they hold a higher memory load. This activity will increase until the individual memory capacity is reached, at which point, the activity will stop increasing for further attempted load increases, creating a plateau in corresponding brain activity. This assumption has been very useful, but it could overlook brain mechanisms that participate in memory but are not modulated by memory load. Another approach may be to examine brain activity related to memory and attention because the retention of information in VSTM has

been suggested to interact with attention (Awh & Jonides, 2001; Baddeley, 1993; Gratton, 1998; Gratton, Corballis, & Jain, 1997; Nobre et al., 2004; Lepsien & Nobre, 2006) through an increase in performance in the recall of information and in activity in areas believed to be implicated in VSTM. Interactions between VSTM and attention are so intricate and pervasive that some propose that both may be different manifestations of the same attentional process directed at different representations (Chun, 2011); VSTM would be attention directed to stable internal representations while visual attention would be attention directed toward volatile sensory representations. The identification of attentional electrophysiological effects during the completion of a memory task would establish a direct relation between attention and VSTM as well as provide a new approach to identify brain activity of interest. This latter approach may pave the way to a different paradigm by focusing on a subset of the information that is most relevant to the participant, instead of the total amount of information retained in memory. This is the approach we explored in the present research, as explained below.

The deployment of attention to an object in the left or right visual field provokes an imbalance in the activity of contralateral versus ipsilateral cortical visual areas in the posterior part of the brain. This cortical imbalance is believed to be created by a greater activation of the cortical areas directly implicated in the visual search task and it can be measured in EEG as the difference in potential observed at posterior electrodes sites across corresponding left and right electrode sites. A peak in this difference is typically found about 250 ms after the onset of a visual stimulus display requiring an attentional deployment to a lateral stimulus. This difference in potential has been coined N2 posterior contralateral (or N2pc), due to its timing in the N2 time range, negative polarity, and posterior contralateral scalp distribution (Luck & Hillyard, 1994). Usually this component is measured as the difference in activity at electrode sites PO7 and PO8, which are at or near the peak of the voltage distribution on the scalp for the component. Recent research has revealed a new imbalance in brain activity, similar in latency and aspect to an N2pc, but this time related to the delayed recall of information in memory (Dell'Acqua, Sessa, Toffanin, Luria, & Jolicœur, 2010; Eimer & Kiss, 2010; Nobre, Griffin, & Rao, 2008). Dell'Acqua et al., in their experiments, presented a memory display

containing an equal number of geometric forms in left and right hemifields simultaneously. After a retention period, the participants were presented a geometric form at fixation and they had to determine if it was present or absent from the initial memory array by a key press. This task introduced an imbalance in voltage scalp activity when the centrally-presented probe matched one of the original forms. This imbalance produced a negative difference wave at electrode sites more anterior than for the N2pc, namely at P7–P8 and T3–T4. These findings have led to the hypothesis that at least part of the visual memory trace is likely to be located in the hemisphere contralateral to the hemifield from which the visual information was initially encoded.

The N2pc component is normally elicited in experimental protocols in which visual arrays are balanced physically, by presenting a target singleton in one visual hemifield and a distractor singleton in the opposite hemifield, to remove possible confounds associated with sensory imbalance, as illustrated in Figure 1(Top). This approach, while most commendable, makes it difficult to disentangle brain activity related to target processing from activity related to distractor processing. A partial solution to this issue has been to isolate lateralized activity to just the target or just the distractor by placing one of them in a lateral visual-field location and the other on the vertical mid-line, as illustrated in Figure 1(Bottom). Stimuli on the mid-line, due to the lateralization calculation, cannot produce differential lateralized activity (Woodman & Luck, 2003), enabling a more precise interpretation of observed lateralized activity to the processing of the lateral item. In such displays, processing is usually restricted to items that are salient relative to other background distractors, which still provide a sensory input balance in term of lateral overall luminance. Using a similar approach, Hickey, Di Lollo, and McDonald (2009) argued that the N2pc could be decomposed into two subcomponents, a negativity contralateral to the target (N_T) and a positivity contralateral to the distractor (P_D) by alternatively positioning the distractor and the target on the vertical mid-line and by observing the difference waveform resulting from the activity related to the lateral target and to the lateral distractor separately. They argued that the sum of these two effects would produce the N2pc wave typically observed in the presence of displays that contain a salient target in one

visual field and a salient distractor in the opposite hemifield (e.g., Jolicœur, Brisson, & Robitaille, 2008).

The sustained posterior contralateral negativity (SPCN; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006), observed by Klaver, Talsma, Wijers, Heinze, and Mulder (1999) and called the contralateral negative slow wave (CNSW), was later also studied further under the rubric contralateral delay activity (CDA; Vogel & Machizawa, 2004), is an electrophysiological component believed to reflect the representations held in VSTM (Klaver et al., 1999). For the duration of the retention interval, the SPCN has been shown to increase in amplitude proportionally to the number of items held in VSTM (McCollough, Machizawa & Vogel, 2007; Robitaille, Grimault, & Jolicœur, 2009; Robitaille et al., 2010; Vogel & Machizawa, 2004). The SPCN is typically observed over posterior electrode (typically PO7–PO8) suggesting a posterior site for the brain structures holding representations in VSTM. We hypothesize that the event-related lateralization found by Dell'Acqua et al. (2010) is due to a reactivation, or an increase in activation, of a memory representation that preserves structural properties of the original sensory input, most notably the visual field at the time of encoding. When attention is deployed to such a memory representation at the time of a search through VSTM, a lateralized ERP reflecting the structural properties of the representation emerges. It is not entirely clear why the scalp distribution of this activity is more anterior than the distribution typically observed for the SPCN for visual information retention, but some brain structures implicated in retrieval from VSTM are likely to be more anterior than the structures involved in visual search or visual information retention (Chun, 2011). Overall, the patterns of results suggest that a careful study of the brain activity observed during retrieval is likely to reveal distinct brain structures from those involved primarily in pure maintenance of representations in VSTM.

In the present work, we used the approach developed by Woodman and Luck (2003) and Hickey et al. (2009) to isolate target-related and distractor-related processing during

VSTM retention and subsequent retrieval. The paradigm allowed us to demonstrate that the N2pc-like component observed during memory recall by Dell'Acqua et al. (2010) is related to an attentional bias toward the target rather than the distractors, and that the results support a view of VSTM as holding the representations of a visual scene items with a dominance in the cortical hemisphere contralateral to the hemifield from which a specific item representation was encoded (Gratton et al., 1997).

Experiment 1

Method.

Participants.

Participants completed the experiments voluntarily and received monetary compensation. They had normal or corrected to normal vision, were neurologically normal, and were not taking neurologically-active medication. There were 26 participants in Experiment 1, 16 of which were kept for analysis (8 women) with a mean age of 23.1 (19 to 29 years old). Forty-six participants completed Experiment 2, 19 of which were kept for analysis (11 women) with a mean age of 23.1 (18 to 32 years old). The large amount of discarded participants was due to very strict rejection criteria for maintaining strict fixation on a central point during the trials, for technical reasons that will be detailed later. All participants signed an informed consent form following the Université de Montréal ethics committee guidelines.

Stimuli.

Each search display consisted of ten equiluminant circles (13.07 ± 0.1 cd/m^2) positioned on a larger circle around the fixation point. Each circle had a diameter of 1.5° of visual angle and the center of each circle was positioned at 4° of visual angle from the fixation point. Two circles were on the central vertical meridian and two circles were in each quadrant, with no circle on the horizontal mid-line (Figure 1). Each circle contained a line with a length

of 0.9° of visual angle at one of four possible orientations (horizontal, vertical, 45° oblique to the left oblique, or 45° oblique to the right). All circles were gray with the exception of two circles, one red and one green. The positions of the red and green circles were varied from trial to trial. In Experiment 1, the red and green circles were aligned horizontally on opposite sides of the central fixation in mirror-symmetric positions immediately above or below the horizontal mid-line (illustrated in Figure 1(Top)). In Experiment 2, one of the colored circles was on the vertical meridian, at the 12 o'clock or the 6 o'clock position, and the other one was in the left or right hemifield, at the position closest to the horizontal mid-line in one of the quadrants on the opposite side to the circle on the vertical meridian (i.e., always a distance of 3 positions in the array of circles, as illustrated in Figure 1(Bottom)).

<<< INSERT FIGURE 1 HERE >>>

Task.

The participant started each trial by pressing the space bar. Trials started with the disappearance of feedback from the previous trial and the presentation of a fixation point. The fixation point remained visible throughout the trial until the feedback was presented. The search display (Figure 1) appeared 400 ms to 600 ms after the space-bar press and was presented for 400 ms. The participant had to remember the stimuli for 1000 ms, from memory array offset, before a colored circle (probe) was shown at fixation. This empty probe circle had the same color as one of the two colored circles presented in the search display and remained in view until a response was recorded. The task was to recall the orientation of the line inside the circle in memory that matched the color of the probe circle and to press a response key corresponding to this orientation with instructions to answer quickly and accurately. Across this paper we will refer to the probed singleton as the target while the other singleton will be referred as the distractor though both singletons had the same status until the probe was presented, both needing to be encoded and maintained in VSTM. Hand of response was counterbalanced between participants; left hand answers were given with the {x, c, v, b} keys while right hand answers were given with the {n, m, ',', '.'} keys on a North American QWERTY keyboard, each key corresponding, respectively, to the line orientations {tilted to the left, vertical, horizontal, tilted to the right}. The participants were given 3000 ms to

answer. Once they answered, accuracy feedback was presented at fixation until the next trial and for a minimum duration of 500 ms. Participants completed 1 block of 32 practice trials followed by 8 blocks of 128 experimental trials (for a total of 1024 experimental trials).

Recordings and analysis pre-processing.

The electroencephalogram (EEG) was recorded with 64 active scalp Ag/AgCl electrodes (BioSemi ActiveTwo system) mounted on an elastic cap. Positioning and naming of the electrodes followed the International 10/10 System (Sharbrough et al., 1991). Data was digitized at a sampling rate of 256 Hz, low- pass filtered online at 67 Hz, and band-pass filtered offline between 0.05 Hz and 30 Hz. The EEG was re-referenced to the average of left and right mastoid electrodes. Trials with a correct response were segmented and averaged for both experiments as 2200 ms long waveforms aligned to the presentation of the memory array, with the preceding 200 ms as baseline for the analysis of pre- probe waveforms, permitting an analysis of the topography of the N2pc/SPCN for the memory array. For post-probe analysis, an 800 ms segmentation was time- locked to the probe presentation, with a 200 ms baseline preceding the probe to remove any previous lateralization not directly related to processing of the probe. Horizontal oculogram (HEOG) was recorded and computed as the difference between signals at additional two electrodes located on the external canthi of each eye. Vertical oculogram (VEOG) was recorded and computed as the difference between signals at an electrode located above (FP1) and an additional electrode below the left eye. Two additional electrodes were used to record signals at the left and right mastoids, and all signals were re-referenced in post-recording analysis to the average of the voltage at the mastoids. Trials with blinks were rejected based on VEOG variations of more than 50 μV in a 200 ms time-window scrolled throughout each trial segment duration. Trials with eye movements, defined as HEOG variations larger than 35 μV in a 200 ms time-window scrolled through each trial segment, were rejected. We rejected data from participants who had less than 50% trials retained after removing incorrect responses and trials with blinks or eye movements, or who had a mean HEOG difference larger than 4 μV across left and right lateral stimulus trials when trials were split across experimental conditions (that would indicate a deviation of the eyes of

about 1/4 degrees of visual angle towards the lateral stimulus (Luck, 2005). It was important to be especially stringent on the rejection criterion because current research suggests involuntary eye saccades away from remembered singletons position in memory (Belopolsky & Theeuwes, 2011), which could have lateralized the probe, which should be at fixation. In Experiment 1, seven participants were rejected due to the eye blinks and three due to the HEOG residuals suggesting eye movements toward a remembered lateral item. In Experiment 2, six participants could barely do the task (less than 70% success rate), nine were rejected due to blinks during the trials duration and twelve had residual HEOG values suggesting eye movements toward a remembered lateral singleton.

Statistical analysis.

Test values for statistical analysis were obtained by averaging the time-point measurements over a time period surrounding a period of interest for each electrode. This period of interest was usually centered on the time of peak amplitude, for the grand averaged waveform across participants, for a particular component. The width of the averaging period was set to 50 ms to ensure good stability of the estimated waveform amplitude on a subject-by-subject basis. T-tests were performed individually for each electrode pair in order to confirm the reliability of the apparent topography of the components.

Results.

We were principally interested in lateralized ERPs, elicited by the probe stimulus, as a function of the side of presentation of the memory singleton that matched the color of the probe. A first objective was to determine if a central probe would induce a lateralized brain response, similar to the N2pc or SPCN, depending on which memory representation matched the color of the probe (Dell'Acqua et al., 2010). When the probed memory singleton had been shown to the left of fixation, right-sided electrodes were considered as contralateral and left-sided electrodes as ipsilateral. These designations were reversed for trials on which the probed

memory singleton had been encoded from the right visual hemifield. In Figure 2(A), we show the grand average of the subtraction of the ipsilateral waveforms from the contralateral waveforms recorded at electrodes CP5 and CP6. The scalp distribution of the lateralized response, computed from the contralateral minus ipsilateral waves for all lateralized electrodes pairs is shown in Figure 2(B).

<<< INSERT FIGURE 2 HERE >>>

These analyses revealed a component that peaked around 300 ms post probe that was more negative contralateral to the probed memory singleton with a scalp distribution similar to the one found by Dell'Acqua et al. (2010). Bonferroni-corrected t-tests against zero considering all 27 electrodes pairs, revealed a significantly negative ($p < .05$) mean activity during the period between 293 ms and 343 ms post-probe[1] at electrodes pairs P3–P4, F5–F6, and CP5–CP6. The most significant electrode was CP5–CP6, with $t(15)=5.38$, $p<.00008$, $M= -.415\mu V$, $\sigma=.3083$.

The initial contralateral negativity was followed by a contralateral positivity to the target with a different scalp distribution, shown in Figure 3. This other component peaked around 559 ms after the presentation of the probe. A t-test against zero (Bonferroni-corrected for multiple comparisons across five candidate electrode pairs selected from the scalp distribution) for the mean activity of the period between 534 ms and 584 ms post-probe revealed that only P5–P6 reached significance, $t(15)=3.32$, $p<.0047$, $M=.4316\mu V$, $\sigma=.5209$.

<<< INSERT FIGURE 3 HERE >>>

Discussion.

The results of Experiment 1 show that retrieval from VSTM is associated with lateralized brain activity that depends on the side of visual space from which the memory

1 The apparent discrepancy between peak amplitude in the figure and the selected time window for analysis is due to the filtering applied to the figure, which smoothed out a peak that was slightly earlier in the unfiltered data.

representation was initially encoded. Importantly, the retrieval cue for this search of VSTM (the probe) was presented at fixation, and could not, by itself, have produced a lateralized brain response. The present results thus highlight an interaction between the retrieval cue and a lateralized representation in VSTM.

The results replicate and extend those of Dell'Acqua et al. (2010) and similar suggestions by others (Gratton, 1998; Gratton et al., 1997; Lepsien & Nobre, 2006; Nobre et al., 2004). In the study by Dell'Acqua and colleagues the probe matched a representation in VSTM in term of shape, or did not match any representation, and the task was to report whether the item was in memory or not. We extend previous results by showing that color can act as the retrieval cue for a shape feature (line orientation), and thus the phenomenon appears to have some generality in terms of basic visual features. We also performed recordings with about twice as many electrodes as in the Dell'Acqua et al. (2010) study, enabling a more detailed mapping of the voltage distribution on the scalp (Figures 2 and 3). The results confirm that the scalp distribution of the contralateral negativity observed during retrieval of a lateralized object in VSTM is clearly more anterior than that found during the initial retention of information in VSTM (Brisson & Jolicœur, 2007; Jolicœur et al., 2008), which we have called the SPCN elsewhere (Brisson & Jolicœur, 2007; Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2006; Jolicœur et al., 2008, 2006; Robitaille, & Jolicœur, 2006; Robitaille, Jolicœur, Dell'Acqua, & Sessa, 2007). Given the clear difference in distribution from the SPCN, and also N2pc, we will refer to this brain response as the TCN, for temporal contralateral negativity.

Experiment 2

In Experiment 2, we aimed to determine if the TCN observed during retrieval in Experiment 1 was due to retrieval of target information from VSTM, per se, to activation and/or suppression of the distractor in VSTM, or to some combination of both. We achieved this by placing either the target or the distractor on the vertical meridian at the time of

encoding. With only one lateral singleton in each trial, we expected to see a contralateral negativity associated with singleton processing shortly after initial encoding (Hickey et al., 2009), and later during the retention interval. Until the probe was presented, however, the participants did not know which of the two singletons would be the target. Hence, we expected to detect an initial N2pc (or N_T, Hickey et al., 2009) and an SPCN, when either the distractor or the target was lateral, until the presentation of the probe. Once the probe was presented, if the TCN activity was related to the target rather than the distractor, we expected to see a negative component for the lateral target condition and, either no activity or positive-going activity in the condition with the lateral distractor, given that Hickey et al. (2009) argued that processing related to distractor suppression is observed as a contralateral positive component (P_D).

Results.

The results immediately following the presentation of the memory array were clearcut: lateral colored circles, that later became either target or distractor, generated an N2pc followed by an SPCN at posterior electrodes, with a maximum near PO7–PO8 and P7–P8. Prior to the presentation of the probe, these waveforms should be equivalent, and this was confirmed by a t-test against 0 of the difference in mean voltage of the lateralized waves for targets and distractors which showed no significant results, the most significant electrode pair FC1–FC2 failed to reach significance, $t(18)=1.80$, $p<.09$.

In order to distinguish the topography of the TCN component from the initial N2pc and SPCN observed during the retention interval, we compared their voltage scalp distributions. We can see from Figure 4(A), showing the activity of the electrode pair CP5–CP6 during the retention period for both experiments, that there was an N2pc/SPCN only for Experiment 2. In Figure 4(B), we can see that the topography of the SPCN for Experiment 2 was more posterior than the TCN. Although the TCN is similar to the N2pc/SPCN in timing, the topography of the TCN is more anterior on the scalp based on visual inspection. Confirming this topography

difference is important because it would contribute to the demonstration that they may reflect distinct underlying processes. We used the mean voltage around the peak amplitude time-point, across lateral target and distractor trials, from 227 ms to 277 ms for the N2pc and from 641 ms to 691 ms for the SPCN, after the presentation of the memory display to compare them with the mean voltage for the TCN component from Experiment 1. We compared the TCN from Experiment 1 with the N2pc/SPCN from Experiment 2 because in Experiment 1 the balanced memory array did not generate any N2pc or SPCN, while Experiment 2 do not produce, in a single condition, a complete TCN (as is shown below). We normalized the voltage of the electrodes sites by component (McCarthy & Wood, 1985). An ANOVA, Greenhouse–Geisser corrected, with the factors Electrode X Component showed no significant Electrode X Component interaction between the N2pc and the SPCN ($F(26\ (6.9), 936\ (249.6))=0.48$, $p<.85$) indicating that both components had a similar scalp distribution. We averaged the N2pc and SPCN voltages to compare them to the TCN voltage on four diagnostic electrodes pairs: PO7–PO8, P3–P4, F5–F6, and CP5–CP6. These electrode pairs were chosen because they captured activity at the peak of the N2pc/ SPCN (PO7–PO8) and the peak for the TCN in Experiment 1 (P3–P4, F5–F6, and CP5–CP6). An ANOVA, Greenhouse–Geisser corrected, with the factors Electrode X Component showed a significant Electrode X Component interaction ($F(3\ (2.8), 99\ (91.8))=2.96$, $p<.04$) confirming what was visible by eye, namely that the TCN had a more anterior/temporal distribution than the typical N2pc or SPCN. While the normalization technique may provide some hint toward separation of brain processes, this technique still has limitations that demand restraint in the conclusions that can be drawn, particularly for inferences about brain generators (Urbach & Kutas, 2002).

<<< INSERT FIGURE 4 HERE >>>

When we inspected the voltage maps in Experiment 2 as a function of the type of lateral singleton (target vs. distractor), a clear difference between conditions (Figure 5(B)) at the time corresponding to the TCN component in Experiment 1 (293–343 ms post-probe) emerged. In the condition with a lateral target, we saw a large fronto-temporal negative component and a small positive component near P7–P8, whereas in the other condition, with a lateral distractor, there was only a large positive component near P7–P8, and no hint of a

fronto-temporal negativity. A Bonferroni correction over all electrode pairs was too conservative for the amplitude of the components observed in the Experiment 2. However, because the components under study had the same general topography as in Experiment 1, and as in previous publications (e.g., Dell'Acqua et al., 2010), we argue statistical reliability is well supported by examining electrode pairs in the same area covered by the TCN in Experiment 1 or at the expected peak of the N2pc. An uncorrected t-test against zero showed for the lateral target condition that negative activity was significantly non-null at T7–T8, C5–C6, FC5–FC6, F7–F8, and CP5–CP6, with peak significance at T7–T8 ($t(18)=2.45$, $p<.025$, $M=-.3529\mu V$, $\sigma=.5326$). For the lateral target condition the positive component failed to reach significance on an uncorrected t-test against zero. The most significant electrode pair was PO7– PO8 ($t(18)=1.58$, $p<.133$). In the lateral distractor condition, positive activity was significantly non-null at TP7–TP8, PO7–PO8, P5–P6, P7–P8, and O1–O2, according to an uncorrected t-test with the peak of significance at P7–P8 ($t(18)=4.97$, $p<.0001$, $M=.6777\mu V$, $\sigma=.5946$). On a paired t-test, we found that P7–P8, near the peak of the positive component in the lateral distractor condition, was not significantly different between the two conditions ($t(18)=1.79$, $p<.09$, $M_D=.6777\mu V$, $\sigma=.5946$, $M_T=.2787\mu V$, $\sigma=.7969$), while the difference between conditions at T7–T8, the peak of the negative component in the lateral target condition, was well above significance ($t(18)=3.73$, $p<.002$, $M_D=.2086\mu V$, $\sigma=.5443$, $M_T=-.3529\mu V$, $\sigma=.5326$). Paired t-tests also showed that conditions differred significantly at electrode pairs TP7–TP8, CP5–CP6, P5–P6, FC5–FC6, F3–F4, and C5–C6, with a peak significance at C5–C6 ($t(18)=3.023$, $p<.007$). The lateralization of the distractor produced a positivity at P7–P8, while the lateralization of the target produced a negativity at T7–T8. We note that the target lateralization also produced a near significant positivity at P7–P8. Figure 5(A) shows the waveforms for electrode pairs CP5–CP6, which was the peak of the TCN in Experiment 1 and which reveals a similar negative going component for the lateral target trials as the peak at electrode pair T7–T8 (not shown), and P7–P8, which is the most significant electrode pair for the positive going component when we had a lateral distractor.

<<< INSERT FIGURE 5 HERE >>>

In order to compare the ERLs of the Experiment 1 TCN with the results obtained in Experiment 2, we subtracted the ERLs of the lateral distractor condition from the ERLs of the lateral target condition. This provided the algebraic equivalent to the Experiment 1 ERLs calculation where both target and distractor were positioned in opposite visual hemifields. When we computed this difference waveform, between 293 ms and 343 ms we found a scalp voltage topography that was very similar to the one obtained for the TCN component in Experiment 1, as can be seen in Figure 6. In this case, the P7–P8 positivity found in both the lateral target and distractor conditions disappeared. The lateral target condition positivity being smaller than the lateral distractor condition positivity, the subtraction actually turned these positivities into a negativity contralateral to the target when algebraically reconstituting the balanced condition of Experiment 1. This clearly illustrates the difficulty of allocating a sign to ERLs without a methodology for isolating the activity source; a negativity contralateral to a target could in fact be a positivity contralateral to a distractor, the other way around, or a combination of both. When we tested the most significant pair of electrodes in Experiment 1 (CP5–CP6) for the difference waveform of the two conditions with a t-test against zero, we found that the mean voltage of the difference waveform was significantly negative ($t(18)=2.39$, $p<.014$, $M=-.449\mu V$, $\sigma=.8175$). This confirmed that we had a greater negativity contralateral to the lateral item at electrode pair CP5–CP6 when we lateralized the target than when we lateralized the distractor. The electrodes with the largest difference between the two conditions in this experiment for this time period was T7–T8 ($M_T=-.32\mu V$, $\sigma=.57$; $M_D=.27\mu V$, $\sigma=.57$; $t(18)=3.53$, $p<.001$). We again found a positive component in the period between 534 ms and 584 ms post-probe, as we had in Experiment 1, for both the lateral target and the lateral distractor conditions scalp distributions. We do not show separately the scalp distributions from Experiment 2, which are very similar to the one found in Experiment 1 and shown in Figure 3. Both maps showed a parietal- occipital positivity, and if anything the lateral distractor condition positive component seemed to be a bit more anterior than the lateral target condition component. An uncorrected t-test against zero revealed that the voltage in the lateral target condition was significantly positive at the electrode pairs O1–O2, P1–P2, P3–P4, P5–P6, P7–P8, P9–P10, PO3–PO4, and PO7–PO8, with a significance peak at PO7–PO8 ($t(18)=5.69$, $p<.00002$, $M=.8589\mu V$, $\sigma=.6577$). In the lateral distractor condition, significantly

positive activity was found with an uncorrected t-test against zero at electrode pairs P3–P4 and P7–P8, with a significance peak at P3–P4 ($t(18)=2.63$, $p<.017$, $M=.3041\mu V$, $\sigma=.5043$). Positive activity was however larger in amplitude in the lateral target condition. The subtraction of both conditions left a scalp voltage distribution with a positive component near PO7–PO8. Positive activity was significantly greater in the lateral target condition than corresponding activity in the lateral distractor condition at the electrode pairs O1–O2, P1–P2, and PO7–PO8, with a significance peak at PO7–PO8, as confirmed by a t-test against zero ($t(18)=3.69$, $p<.002$, $M_D=.1739\mu V$, $\sigma=.4176$, $M_T=.8589\mu V$, $\sigma=.6577$). One surprising exception was found at F5–F6, where voltage was significantly lower in the lateral target condition than in the lateral distractor condition ($t(18)=2.2$, $p<.041$, $M_D=.3856\mu V$, $\sigma=1.0502$, $M_T=-.1861\mu V$, $\sigma=.613$).

<<< INSERT FIGURE 6 HERE >>>

From 141 ms to 191 ms post-probe there was a positive component that was very similar in scalp distribution across the two conditions (Figure 7). The component was significantly different from zero at PO7–PO8 (post-probe, target: $t(18)=6.75$, $p<.000002$, $M=.7328\mu V$, $\sigma=.473$; post-probe, distractor: $t(18)=6.42$, $p<.000005$, $M=.5414\mu V$, $\sigma=.3678$) when comparing mean activity between 141 ms and 191 ms. A paired t-test between conditions showed the conditions to be nearly significantly different ($t(18)=2.00$; $p<.06$). Also, this component had a similar scalp distribution to a component seen between 141 ms and 191 ms after the presentation of the memory array. We normalized the voltage of the electrodes sites for the post memory array component and the post probe component (McCarthy & Wood, 1985). An ANOVA, Greenhouse–Geisser corrected, with the factors Electrode X Component showed no significant interaction Electrode X Component ($F(26\ (7.1), 468\ (128))=1.89$, $p<.08$) suggesting, since the null hypothesis was not rejected, that both components had a similar scalp distribution.

<<< INSERT FIGURE 7 HERE >>>

Discussion.

Experiment 2 brought several interesting findings. First, we again found a clear contralateral negativity with a more anterior scalp distribution (a TCN) relative to an SPCN, when we probed VSTM with a centrally-presented probe and the target was encoded from a lateral spatial location. This finding extends those of Experiment 1 by showing that the TCN can reflect lateralized activity related to the position of the target, without contamination from distractor processing. The target-related TCN can also be found when retrieval from VSTM is performed on the basis of a color cue, extending the results of Dell'Acqua et al. (2010), who studied a shape-matching retrieval process.

Importantly, Experiment 2 also produced new findings. Relatively early after the presentation of the central retrieval cue (between 141 ms and 191 ms), we observed a posterior positivity contralateral to the lateral item in VSTM, whether that item matched the retrieval cue or not (i.e., was the same for lateral targets as for lateral distractors). A similar component has been observed following the presentation of visual displays containing a lateral item 'of interest' even when that item is balanced by a luminance-matched item 'of lesser interest' on the other side. A visual salience imbalance could be responsible for this component presence. For example, in the present Experiment 2, the two interesting items were those colored red or green, compared to the grey ones, even though they were all equally luminant. We will refer to this component, when observed following the initial presentation of a physical display, as the Ppc (positivity, posterior contralateral). A similar Ppc has been observed in a number of studies (e.g., Leblanc, Prime, & Jolicœur, 2008; Sawaki & Luck, 2010), although it has not been the focus of much research so far. From those studies and our Experiment 1, the Ppc appears to reflect an initial processing of the display based on local feature discontinuities, which may guide later controlled deployment of visual spatial attention, reflected in the N2pc. It is particularly interesting that we observed a similar response following the presentation of the memory cue, at fixation, based on the memorized lateral position of stimuli held in VSTM. This result lends further support for the notion that VSTM can preserve a spatially isomorphic representation of visual stimuli, likely based on a spatiotopic mapping of external space in the brain. The fact that we appeared to find a memory-based Ppc following the presentation of the

probe, and that this response was similar for probes that matched a lateral target or a lateral distractor suggests that there was likely an initial reactivation of the entire memory representation (i.e., of both the target and distractor) and that the Ppc may be a spatial index linked to a representation of interest rather than a reflection of a perceptual discontinuity in the visual array information.

General discussion

With a balanced display in Experiment 1, we replicated and extended the most important findings of Dell'Acqua et al. (2010). We found a contralateral negativity during retrieval from VSTM that was widespread, spanning from P3–P4 to F5–F6, with a peak near CP5–CP6. Because of the structure of our experiment, in which the retrieval cue was displayed at a central fixation point, this voltage imbalance between the contralateral and ipsilateral hemispheres relative to the position of memorized stimuli could only be the reflection of a differential activation of some of the neural structures implicated in the retention of lateralized information in VSTM. The representation itself must, in some sense, have preserved the differential activation of lateralized brain activity produced by the stimulus at the time of encoding. The results observed by Dell'Acqua et al. (2010) had a component that peaked at more inferior electrode sites than we found in our Experiment 1, and closer to the peaks observed in Experiment 2 at P7–P8 and T7–T8. However, the spatial sparsity of these earlier recordings may explain this discrepancy in peak location. Another possibility is that the variation of the component morphology could reflect the differences in stimulus materials (simple shapes in the Dell'Acqua et al., 2010, study, vs. color and line orientation in the present study). Importantly, the lateralized component observed during retrieval does not match the scalp distribution of the N2pc or SPCN found in typical studies of visual attention (e.g., Brisson & Jolicœur, 2007; Jolicœur et al., 2008) or of the SPCN found during the initial maintenance of representations in VSTM for the retention interval in Experiment 2. Thus, we confirm one of the most important findings of Dell'Acqua et al., namely the more temporal distribution of the lateralized activity related to retrieval, which we now call the TCN. It is likely that the TCN reflects distinct, and possibly more anterior, generators engaged in

retrieval from VSTM, than those required for the initial selection, encoding, and maintenance of visual representations. The balanced visual display of Experiment 1 and the baseline correction preceding the presentation of the probe in Experiment 2 both ensure that the observed TCN activity is distinct from the activity related to memory maintenance producing the SPCN. However, there is still a possibility that the activity of the TCN reveals an increased activation of generators already active during the SPCN and that are masked by stronger posterior generators.

In order to ensure that the TCN following the probe was due to attentional and retrieval processes related only to the target rather than a partial contribution to the effect from both target processing and distractor suppression, we isolated lateralized activity related to the target and to the distractor in a second experiment. Experiment 2 was identical to Experiment 1 except that the memory array had one of the two colored circles on the vertical meridian. The lateralized differences we then obtained originated from the singleton that was lateral because any effect that would have been generated by the midline singleton would have been canceled in the subtraction used to compute interhemispheric differences across matched lateral electrodes. Since both colors and positions were randomly attributed, trial by trial, to the target or to the distractor, the only factor that was uniquely associated with our manipulations was the lateralization of representations in the brain, and consequently of the deployment of attention, at the time of retrieval.

The voltage scalp distribution observed in the lateral target condition of Experiment 2 (Figure 5(B) top) confirmed that the TCN was related to the retrieval of the target item representation in VSTM. A fronto-temporal negative component was only present when the target was lateral, which differentiated the TCN from more perceptual components, such as the N2pc and SPCN. This spread of activity across more anterior electrode sites when the target was lateral suggests that temporal cortical structures may be involved during the retrieval of visual information held in VSTM, because the activity imbalance related to the retrieval of

information can only be observed in this condition. In addition to the anterior negativity, we observed a contralateral positivity over the posterior scalp in Experiment 2. This posterior positivity near P7–P8, which was only nearly significant when the target was presented laterally, but fully significant when the distractor was presented laterally, could indicate that part of the activity during retrieval is common to both target and distractor related processing. The relatively small amplitude of the positive component, and to some extent of the negative component as well, in the lateral target trials could be the effect of destructive summation of scalp voltage for the two opposite polarity neighboring components. The fact that the TCN peak is located at electrode sites between the two lateral target components peaks and the shape of the components could indicate that the TCN originates most likely from the modulation of a single large component that covers the extent of the TCN voltage scalp distribution in Experiment 1. This spatially-large component (but of relatively weak voltage amplitude) would share a part of the scalp surface occupied by another posterior positive component present and constant when the target and the distractor are lateral. An alternate explanation would be that the two components are modulated alternatively in the same direction, the fronto-temporal negative component when the target is lateral and the parieto-occipital positive component when the distractor is lateral, and that this effect is averaged in Experiment 1 to peak between the individual peaks present in the lateral target condition voltage scalp distribution found in Experiment 2. Due to the distance separating the two opposite polarity peaks, this latter explanation is unlikely because the voltage decay over the scalp would most likely lead to an averaged voltage for the observed TCN peak to be inferior to the average of the two individual peaks modulated across the lateral target and lateral distractor conditions.

The voltage scalp distribution observed in the lateral distractor trials of Experiment 2 (Figure 5(B) bottom) revealed a parieto- occipital positive component and an absence of the fronto- temporal negative component seen in the lateral target condition. This indicates that the TCN represents recall-related activity specifically related to the target that is absent when the distractor was the lateral item. The absence of negative component in the lateral distractor

trials is consistent with the need to access lateralized representations only when the target was lateral. The topography of the parieto-occipital positive component resembles that of the N2pc and SPCN with reversed polarity. Although this positive component could reflect an active inhibition of the memory representation in VSTM of the lateral distractor, this component could also be explained by a return to baseline from a state of sustained activity required to maintain the representation of the distractor during the retention interval prior to the probe. Once the probe was presented and found to match the midline object, the maintenance of the lateral object would no longer be required. The baseline correction introduced on the 200 ms pre- probe period make it so that the voltage was actually negative compared to a pre-memory array baseline. A return to this pre- memory array baseline would be seen as a positive going component, sustained while the target is still in use, resembling a positive SPCN. In the time range of the TCN, both possibilities are credible and more research will be needed to disentangle these possibilities.

In addition to the TCN, we isolated a latter positive going component in the difference waveform of Experiment 1 that had a more occipito-parietal distribution with a peak centered near P5– P6. This latter positive component, present between 534 ms and 584 ms post-probe in the balanced experiment, was elicited by bilateral singletons, one a target the other a distractor. Experiment 2 elicited a similar component in the algebraic difference between the waveforms from the lateral target trials and the lateral distractor trials. While Experiment 1 could not indicate whether the positive component was elicited by the activity generated by the processing of the target, Experiment 2 could show us the activity linked to each singleton separately. In Experiment 2, the late posterior positivity was larger on the lateral target trials than on lateral distractor trials, although it was also seen on these latter trials. This difference between conditions would be equivalent in the balanced experiment to a positive component contralateral to the target. This positive component timing and voltage scalp distribution left us wondering if this component could not be an artifact generated by involuntary eye movements toward the target bringing the probe, still present on the screen, toward the distractor

hemifield. Our severe eye movements rejection criterion should have prevented such an occurrence, however, which leaves us uncertain as to the nature of this component.

In summary, the individual lateral placement of the target and distractor in our memory task in Experiment 2 made it possible to distinguish two components, between 293 ms and 343 ms after the probe presentation. When we summed these effects we observed a pattern that was undistinguishable from what we found in Experiment 1, in which target and distractor were both lateral (in opposite hemifields). Thus, we consistently found a component, we now call the TCN, which is a broadly distributed negative ERL, following the presentation of a central memory probe. The TCN thus appears to reflect a negative component, more anterior, related to the target and a positive component, more posterior, related mostly to the distractor that both confirm the lateralization of the memory structures in VSTM, as well as indicating a dissimilarity in the processing of the target and the distractor at the time of the retrieval. Whereas the more anterior temporal component related to the target could be related to the structures holding the visual information, the more posterior component is close to the regions already linked to the retention of information in VSTM, notably by the research done on the SPCN. This result, combined with results from curve tracing (Lefebvre, Jolicœur, & Dell'Acqua, 2010) and multiple objects tracking (Drew and Vogel, 2008) studies that find an SPCN in paradigms that do not rely on VSTM, suggests that the SPCN, and the posterior positive component, may be present in tasks that require tracking of visual representations in either perception or memory, representations that would be held in other cortical regions. The positive going component in the lateral distractor condition might indicate the disengagement of the structures contributing to the SPCN for the distractor or an active inhibition mechanism in memory for that item. The Ppc, an already known component but little-studied, was observed in the lateralized conditions pre-probe waveforms and, as far as we can tell, also post-probe, altering the reconstitution of the balanced waveform by making a positive deflection in the waveform resulting from the subtraction of the two conditions (Figure 6). The presence of a Ppc like component during retrieval would hint toward a reactivation of cortical structures activated during perception, because the centered probe could not account for an

imbalance in salience, which would elicit a Ppc. As can be seen on Figure 5(A) on the P7–P8 electrode pair, this component is sustained longer during retrieval when the distractor is lateral, which let us wondering if this component could not also be sustained and masked by the overlap in the lateral target condition with the larger negative going component at anterior electrode sites seen on Figure 5(A) at electrode pair CP5–CP6. This would in turn raise the hypothesis that, in perceptual search tasks, the N_T part of an N_T– P_D pair may be superimposed to the P_D, occupying during perception roughly the same scalp area, whereas during retrieval, in a memory task, the target related component would be more anterior than the positive component. The resulting voltage distribution would reveal both the anterior target related negativity and the posterior positivity that could be a spatial index of representations of interest. The Ppc could be the initial part of a larger posterior positive component that remains active throughout the N2pc or the TCN, whose negative-going inflexion mask the posterior sustained activity until its later part, called the P_D, become visible in distractor related trials, when attention toward the distractor is minimal. More generally, the present results suggest we can elucidate the nature of the neuronal representation of visual memory representations and retrieval mechanisms that operate on them by careful examination of electrophysiological waveforms during retrieval, and that event-related lateralizations are likely to be particularly useful in these endeavors.

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Figure Captions

Figure 1. Timecourse of each trial for Experiment 1 (top) in which the colored circles to be remembered were both lateral, in opposite hemifields, and for Experiment 2 (bottom) in which one colored circle was on the vertical midline and the other was in a lateral position.

Figure 2. Experiment 1. A) Grand average of the ERLs recorded at electrodes CP5 and CP6 timelocked to the presentation of the probe band pass filtered between 0.1 Hz and 6 Hz. B) Scalp distribution of the lateralized response, computed from the contralateral minus ipsilateral waves for all lateralized electrodes pairs, showing the mean voltage between 293 ms and 343 ms post-probe.

Figure 3. Experiment 1. A) Grand average of the ERLs recorded at electrodes P5 and P6 timelocked to the presentation of the probe band pass filtered between 0.1 Hz and 6 Hz. B) Scalp distribution of the lateralized response, computed from the contralateral minus ipsilateral waves for all lateralized electrodes pairs, showing the mean voltage between 534 ms and 584 ms post-probe.

Figure 4. A) Grand average of the ERLs recorded at electrodes CP5-CP6 during retention, timelocked to the presentation of the memory array band pass filtered between 0.1 Hz and 6 Hz, in Experiment 1 (dashed line) and in Experiment 2 (solid line). An N2pc and SPCN can be seen for Experiment 2 in which one of the stimuli was lateral and the other was on the midline, but is absent for Experiment 1 in which the two items to be memorized were in opposite hemifields. B) Scalp distribution of the lateralized response (SPCN) in Experiment 2, computed from the contralateral minus ipsilateral waves for all lateralized electrodes pairs, showing the mean voltage between 600 ms and 1400 ms after the presentation of the memory array.

Figure 5. Experiment 2. A) Grand average of the ERLs recorded at electrodes CP5-CP6, to illustrate the target-related negativity, as well as P7-P8, to illustrate the distractor-related positivity, both timelocked to the presentation of the probe, band pass filtered between 0.1 Hz and 6 Hz. B) Scalp distribution of the lateralized response showing the mean voltage between

293 ms and 343 ms post-probe for the lateral target condition (top) and the lateral distractor condition (bottom).

Figure 6. A) Grand average of the ERLs recorded at electrodes CP5 and CP6 timelocked to the presentation of the probe, band pass filtered between 0.1 Hz and 6 Hz, in Experiment 1 (solid line) and in Experiment 2 (dashed line), estimated as the sum of the lateral target and lateral distractor conditions. B) Scalp distribution in Experiment 2 resulting from the the subtraction of the ERLs recorded in the lateral distractor condition from the ERLs recorded in the lateral target condition between 293 ms and 343 ms post-probe for all electrodes pairs. A smaller lateral view of Experiment 1 TCN is provided for comparison.

Figure 7. Results from Experiment 2 showing, from left to right, scalp distributions of ERLs recorded across all electrode pairs showing a Ppc (Positivity posterior contralateral) component between 141 ms and 191 ms post memory array, post-probe in the lateral target condition, and post-probe in the lateral distractor condition.

Figure 1

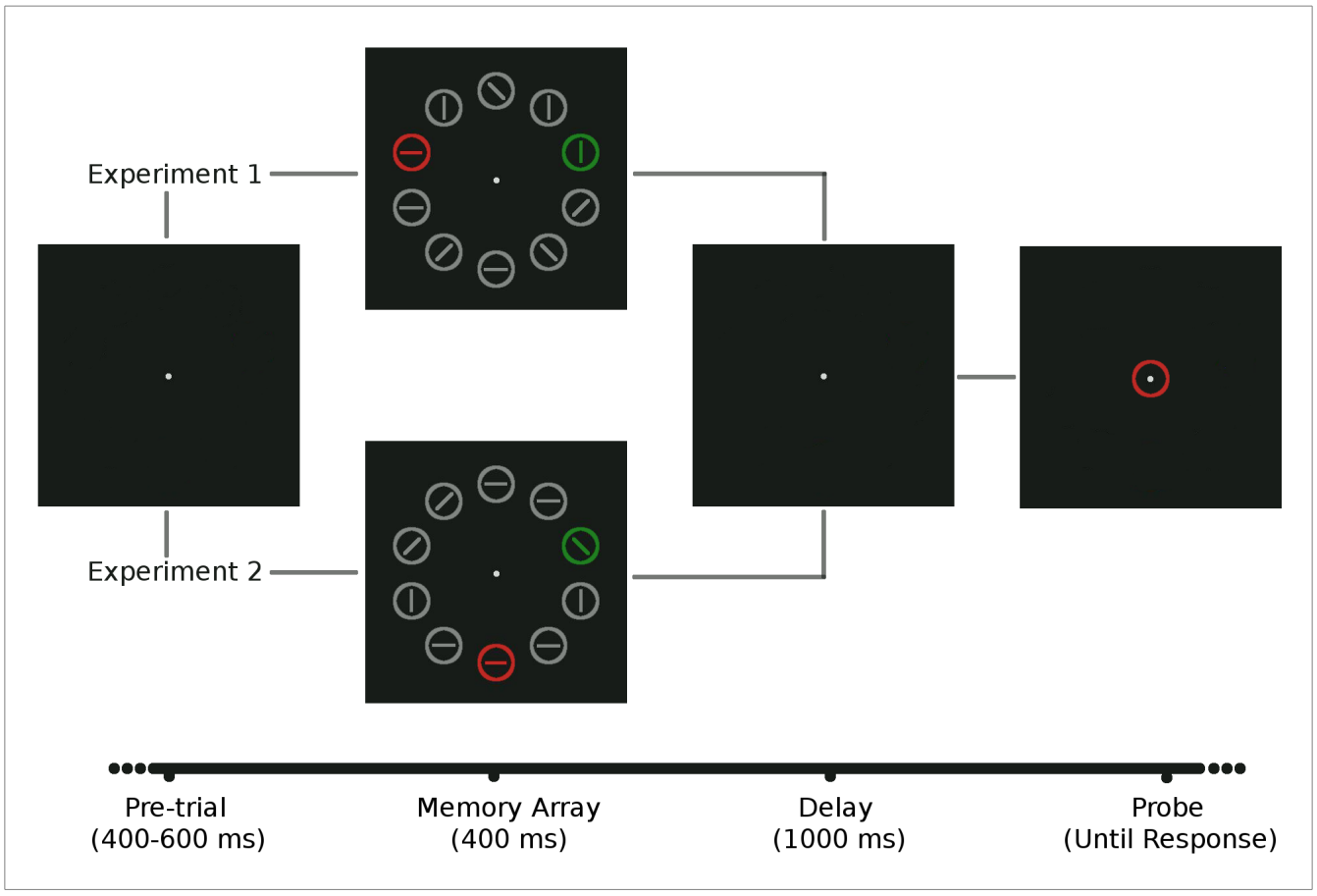

Experiment 1
Experiment 2
Pre-trial
(400-600 ms)
Memory Array
(400 ms)
Delay
(1000 ms)
Probe
(Until Response)

Figure 2

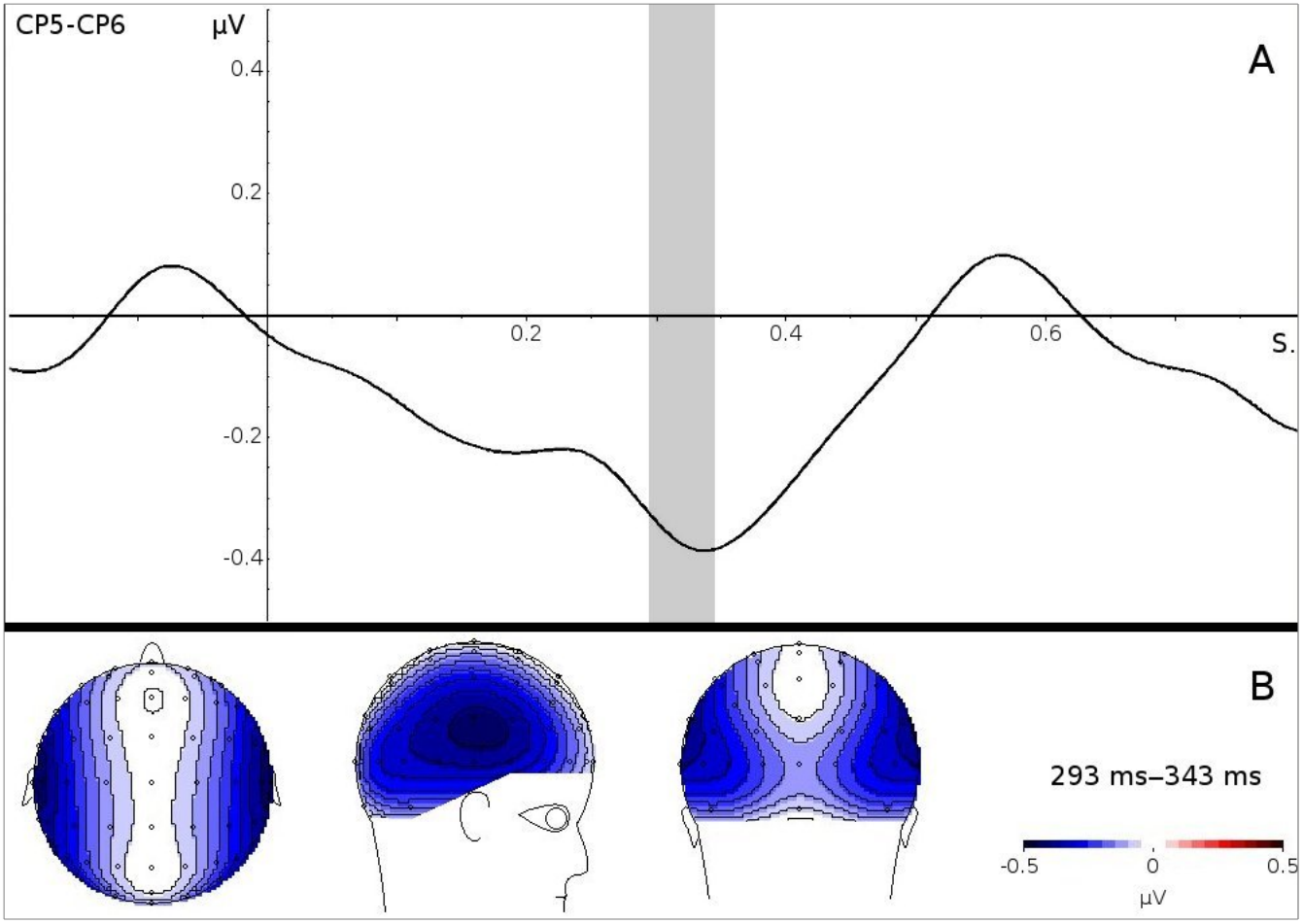


Figure 3

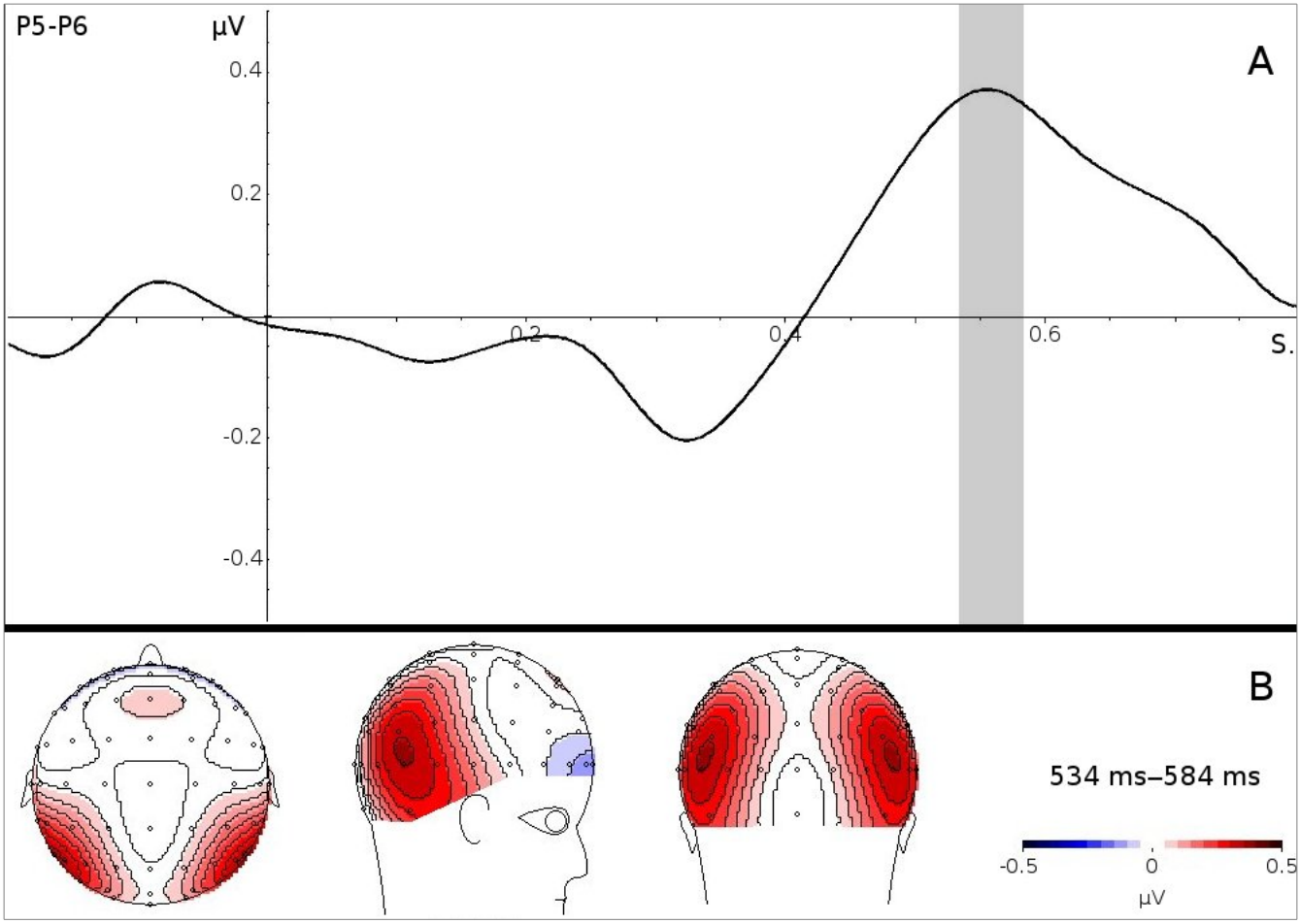


Figure 4

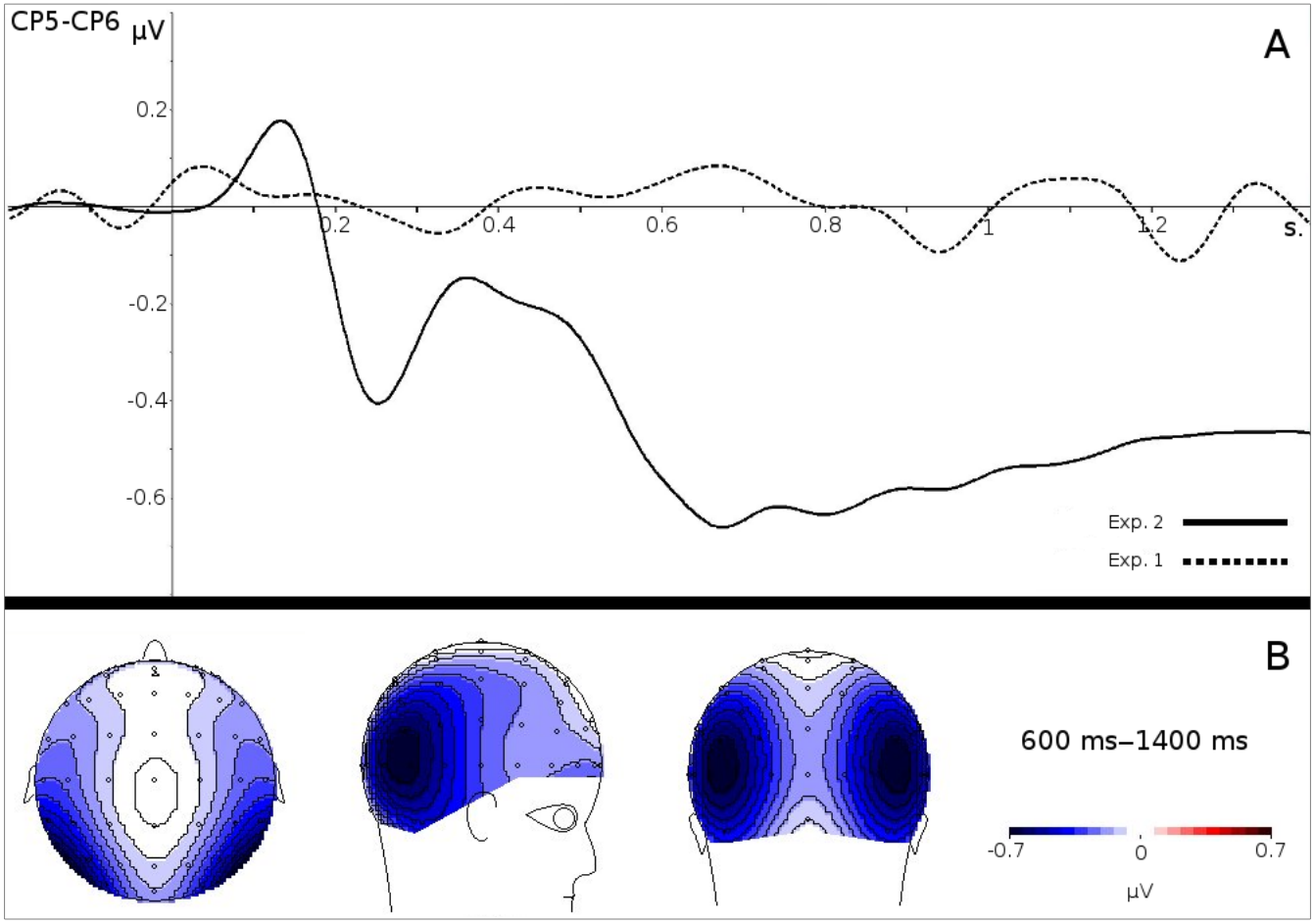

CP5-CP6 µV
A
0.2
-0.2
-0.4
-0.6
0.2
0.4
0.6
0.8
1
1.2
s.
Exp. 2
Exp. 1
B
600 ms–1400 ms
-0.7
0
0.7
µV

Figure 5

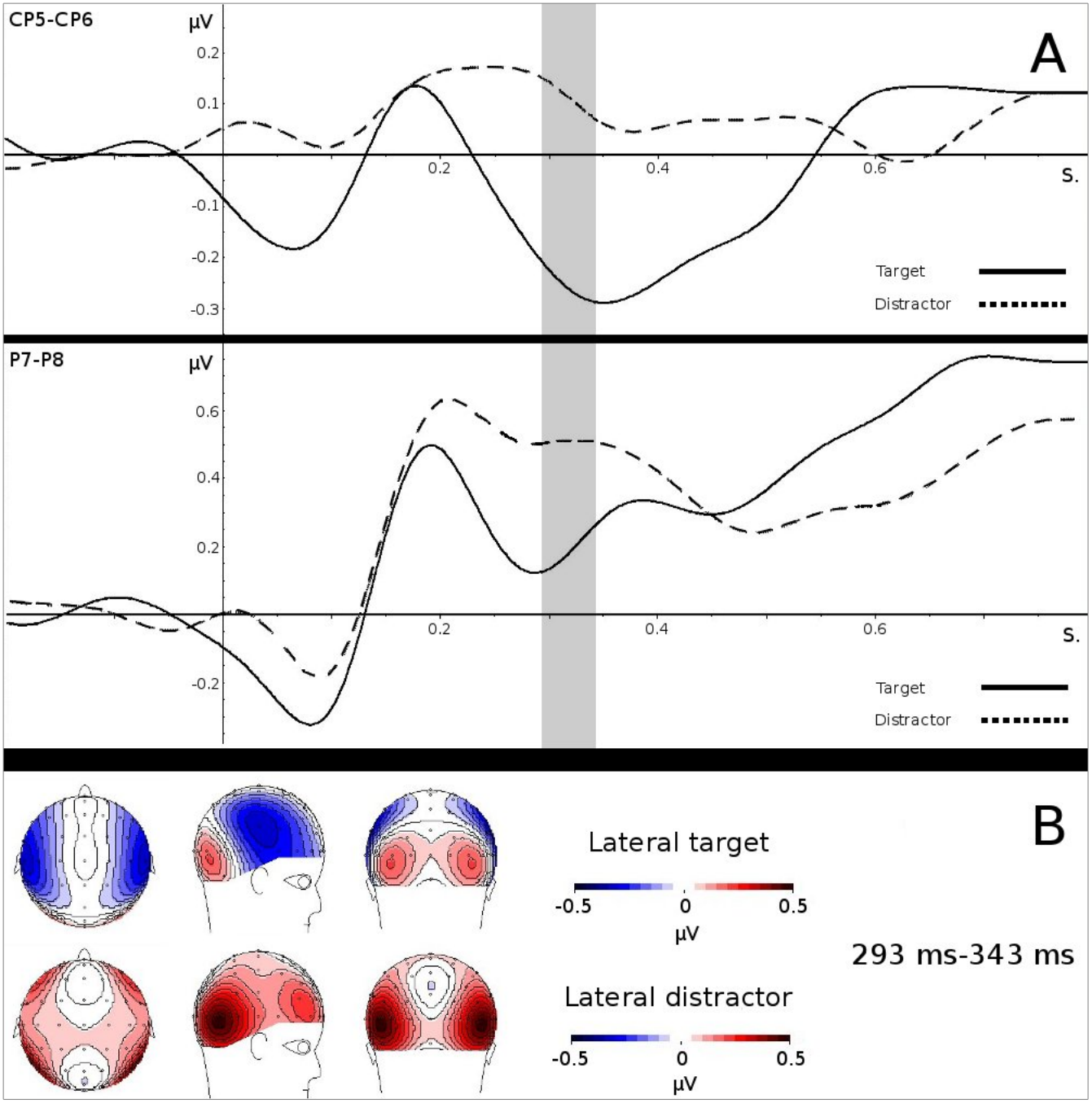

CP5-CP6
µV
0.2
0.1
-0.1
-0.2
-0.3
0.2
0.4
0.6
S.
A
Target
Distractor
P7-P8
µV
0.6
0.4
0.2
-0.2
0.2
0.4
0.6
S.
Target
Distractor
B
Lateral target
-0.5
0
0.5
µV
Lateral distractor
-0.5
0
0.5
µV
293 ms-343 ms

Figure 6

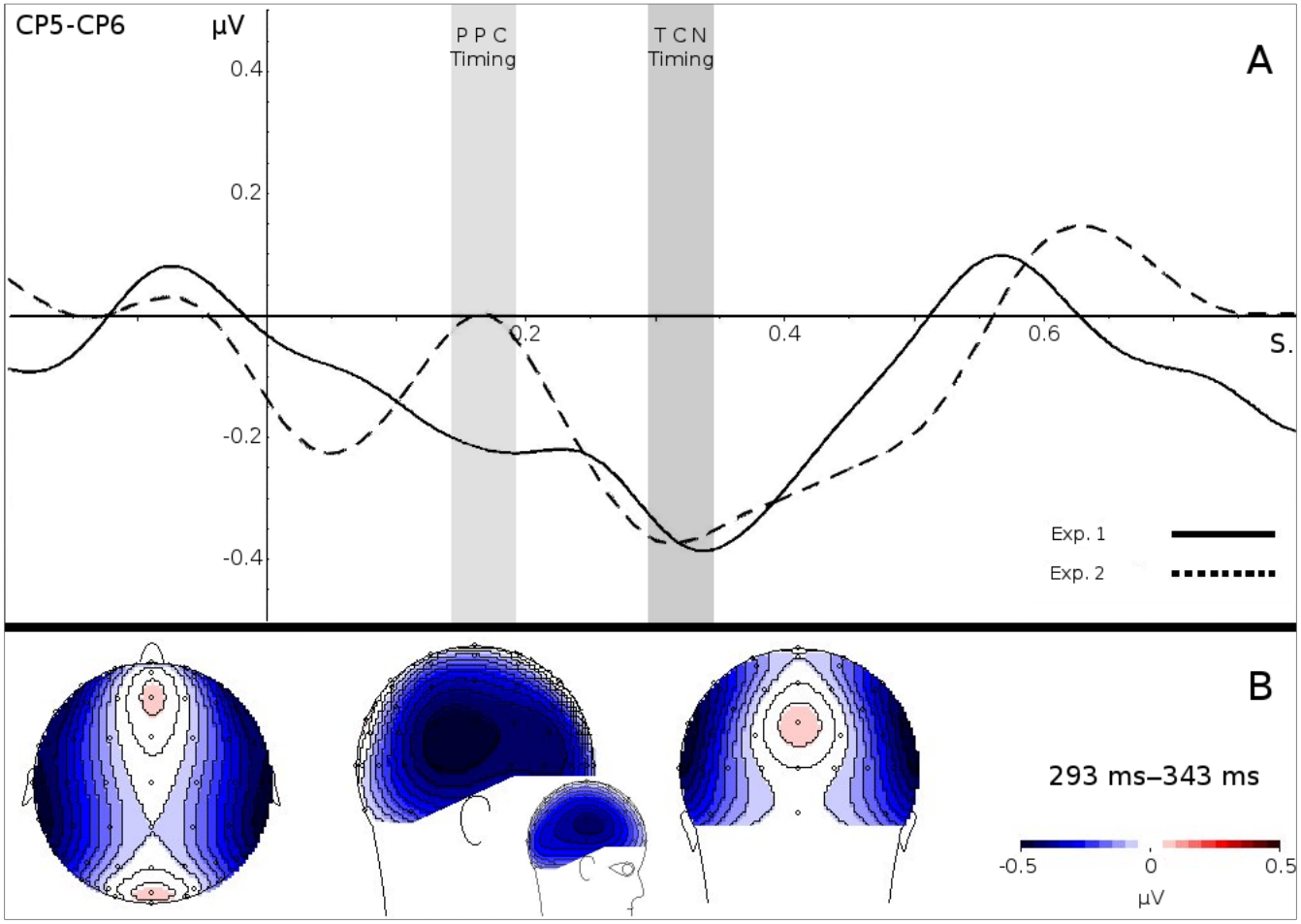
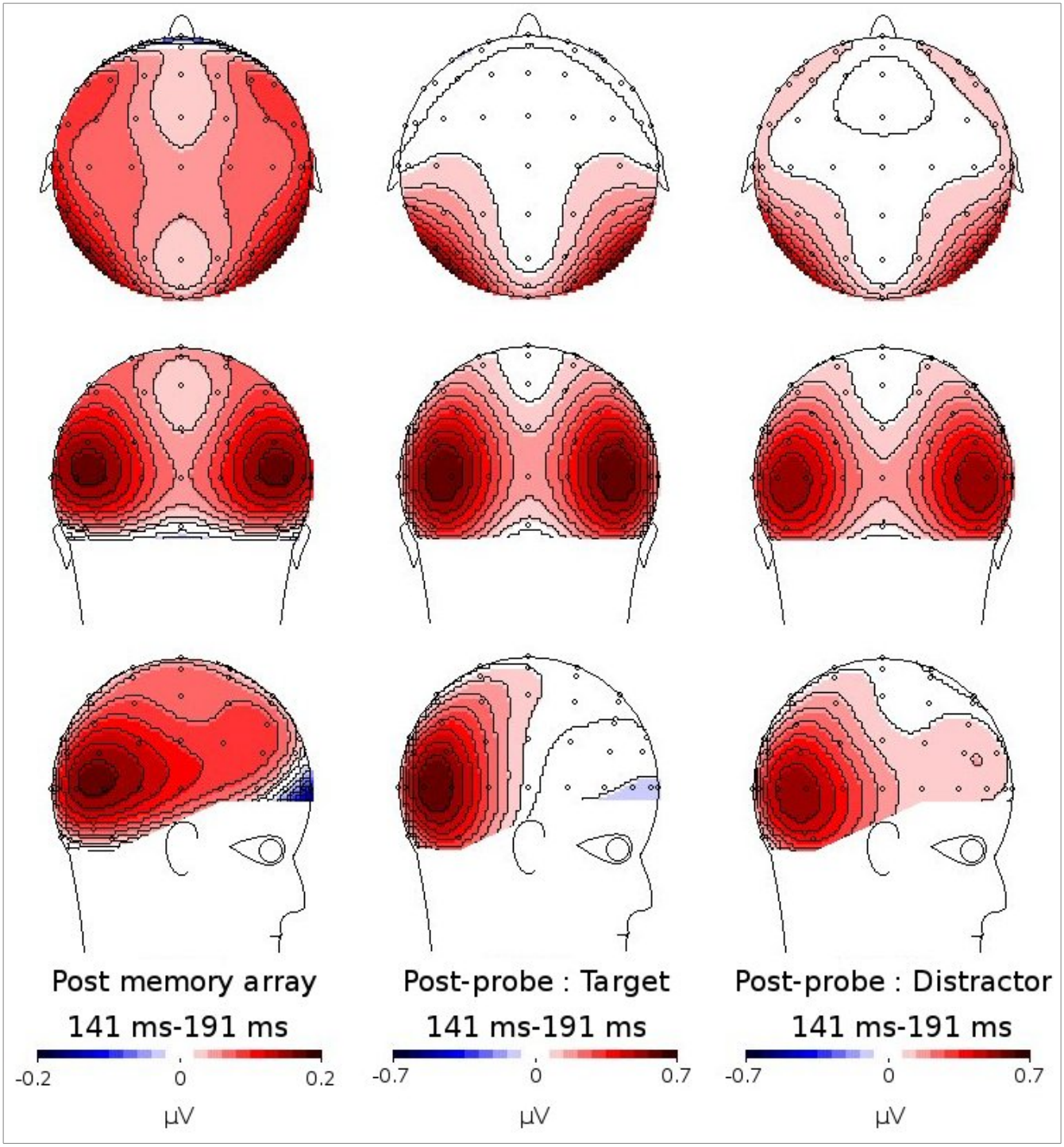

CP5-CP6
µV
0.4
0.2
-0.2
-0.4
P P C
Timing
T C N
Timing
A
0.2
0.4
0.6
S.
Exp. 1
Exp. 2
B
293 ms–343 ms
-0.5
0
0.5
µV

Figure 7


Post memory array
141 ms-191 ms
-0.2
0
0.2
µV
Post-probe : Target
141 ms-191 ms
-0.7
0
0.7
µV
Post-probe : Distractor
141 ms-191 ms
-0.7
0
0.7
µV

Chapitre 3 : Electrophysiological evidence of distractor interference during pop-out visual search

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A friend once elegantly rebuffed my depiction of ogres as lumbering, large, and clumsy creatures, pointing out an obvious fact. For such a creature to exist without being seen implies a level of stealth that flirts with the unnatural. The creature clearly has a knack for hiding in plain sight despite the less than optimal anatomy that was bestowed upon it. Another denizen of our laboratories similarly escapes our scrutiny: the grey distractors in color pop-out visual search tasks used in many experiments. Their inconspicuous nature alongside inconvenient contributions put them at the bottom of the list when it comes to explaining results. While ogres are generally uncooperative by nature, grey distractors are more easily manipulated to restore the place they deserve in theorizing about the role of attention in visual search.

When performing a visual search task, one implicitly expects to search for something: a target. The target is defined by a set of features (alone or in combination) that sets it apart from the other visual elements of the search display: the distractors. A visual search performed on the basis of a single positive feature that can distinguish the target from distractors has been argued to be performed in parallel and pre-attentively (Treisman, 1982). Search time and accuracy are relatively unchanged by the presence or number of distractors, which support this view. Visual attention is often conceptualized as a set of processes that provide the visual system with a way to enhance target-related activity and processing speed over a limited spatial region. When performing a visual search with a target defined by a conjunction of features, search time often increases with each additional distractor (Treisman, 1982), which

has been interpreted as evidence for serial search (Treisman & Gelade, 1980). Regardless of the way the search task is performed, parallel or serial, attention is hypothesized to be deployed to the potential targets to confirm the needed information when an identification is required. The term pop-out search implies that some form of spatial selection is possible immediately on the basis of a feature. In the case of a conjunction of features, further attentional processing is required to combine the information available on each search item of the subset in order to confirm it is a target.

Electrophysiological recordings performed during a search task can provide useful information concerning mechanisms of attention. The N2pc (Luck & Hillyard, 1994), designating a negative component measured around 200 ms post-stimulus on the posterior and controlateral part of the scalp, provides a temporal as well as rudimentary (left-right) spatial index for attentional deployment. The N2pc is calculated by subtracting ipsilateral activity from the controlateral activity at each electrode position. An N2pc indicates the visual hemifield in which the attention is deployed, but does not provide by itself information on the size or precise locus of attented space. Thus, the mere presence of an N2pc does not constrain which part of a visual display is modulated by attentional processing at any given moment during a visual search task. The deployment of visual spatial attention has been likened to a single spotlight (Posner, 1980) or lense that can be adjusted in size (LaBerge, 1983; Eriksen & James, 1986) in accordance to task demands. The singularity of the attentional focus has been questioned. Under specific conditions (queued location targets, opposite hemifields, non-sudden onset distractors) multiple foci may be possible (Castiello & Umilta, 1992; Awh & Pashler, 2000). Heinze et al. (1994) made a compelling argument for the single focus of attention. While directing attention toward two potential target positions, a probe was presented briefly at an irrelevant or relevant position. If an irrelevant position was between two relevant positions, it generated a P1 event-related component similar to the ones obtained for presentation at a relevant position. An irrelevant position probe generated otherwise a smaller P1. Nevertheless, the lack of simultaneous attentional target during the presentation of the probe may have provoked unintentional attentional capture. The size, position, and

possible number of attended regions have been studied extensively and are still a matter of debate and ongoing investigation (Pan & Eriksen, 1993; Hahn & Kramer, 1998; Müller & Hübner, 2002; Müller, Malinowski, Gruber, & Hillyard, 2003).

In any case, experimental results need to be interpreted with caution due to uncertainty concerning the geometry and topology of attended spatial regions. Hilimire, Mounts, Parks, and Corballis (2009) found a larger N2pc amplitude with increasing distance between a colored target and a colored distractor on a circle otherwise occupied by grey distractors. However, they did not consider the fact that increasing the distance between the salient (colored) items also increased the number of grey distractors present in the attended region. They concluded that closer distrators caused lateral competition between cell populations, which reduces the N2pc. They also found that the positivity temporal controlateral (Ptc), an event-related lateralization (ERL) component following immediately after the N2pc, was more positive as the distractor got closer to the target. The Ptc was initially identified as a suppression bias signal used to resolve the competition between attended items, but Hilimire and Corballis (2014) revised that position saying the Ptc was indexing the termination of attentional processing similarly to the distractor positivity (Pd) (Hickey, Di Lollo, & McDonald, 2009) as seen by Sawaki, Geng, & Luck (2012) or the P4pc (Toffanin, de Jong, & Johnson, 2011). In the present paper, we study the effect of grey distractors on N2pc and Ptc time course and use the results to infer the properties of the visual attention system.

By using a visual search display with a distractor sharing the target color, we can create an “area of interest” delimited by those two potential targets (colored items). We can then manipulate the number and position of additional grey distractors to probe the functional properties of the attentional focus without changing the fundamental nature of the visual search task. By using distinct pop-out colors, according to most theories of search, the grey distractors should be easily rejected preattentively. We created a region where attention was needed to further individuate the two potential targets. According to models of attention with a

single attentional focus, the center of the attentional focus should be between the potential targets, spreading over both. However, the focus could, alternatively, move serially from one potential target to the other. The identification of targets, and N2pc, which indexes attentional deployment, should be more disrupted by grey distractors placed between potential targets compared to distractors outside this "area of interest." This disruption is expected to produce an increased latency and/or a reduced amplitude for the N2pc component for conditions with distractors inside the "area of interest." This would indicate an increased time to identify the target and an increased use of attentional capacity. On the other hand, if attention is split in two foci each centered on a potential target, the position of grey distractors should have no effect, and the latency and amplitude effects should be equivalent for an equal number of distractors. Finally, if grey distractors are really neutral in a color visual search task, then there should be no difference of note on N2pc amplitude and latency when adding grey distractors inside and outside the "area of interest" compared to the absence of these distractors. The following experiments tested these various predictions.

Experiment 1

Method.

Participants.

47 Participants, of which 42 were kept for analysis (13 males, average 22.4 years old), completed the experiment voluntarily and received monetary compensation after providing written informed consent. They had normal or corrected to normal vision, were neurologically normal, and were not taking neurologically-active medication according to self reports. Five participants were rejected because their low success rate and eye movements during trials led to less than 40% remaining trials kept. A participant completed only 5 experimental blocks and another participant completed 4 experimental blocks while still meeting the criterion to be kept. The experimental paradigm was vetted by the ethics committee of the faculty of arts and science at Université de Montréal.

Procedure.

Participants were asked to count the number of search frames containing an inverted T displayed in a particular color (green or yellow, which was counterbalanced between participants). Participants started each trial by pressing the spacebar. The first search frame was presented after a 500 ms +/- 100 ms delay and another frame every 900 ms +/- 100 ms of inter-stimulus interval (ISI) until 6 search frames were presented, as illustrated in Figure 1C. Frame presentation duration was 200 ms. After the last frame was presented, participant had 3000 ms to answer by pressing with a single hand the correct count between 4 possible alternatives (3, 4, 5, or 6). The keyboard keys used for their response were respectively, for a count of 3, 4, 5, or 6, {'b', 'v', 'c', or 'x'} for participants responding with the left hand or {'n', 'm', ',', or '.'} for participants responding with the right hand, on a North American QWERTY keyboard. Hand of response was counterbalanced between participants. Feedback on response accuracy was shown at fixation (+ or – signs) after the response was given for 500 ms. Throughout each trial, composed of six search frames, participants had to keep fixation on a central dot that remained on the screen for the whole trial. Each participant completed 1 block of 12 practice trials followed by 6 blocks of 96 experimental trials, for a total of 3456 search frames.

<<< INSERT FIGURE 1 HERE >>>

Stimuli.

Each search frame had 16 positions for letters of 1.2° by 1.2° of visual angle positioned around an imaginary circle with a diameter of 12° of visual angle, with a fixation dot at the center. All letters were 2.3° apart center-to-center from letters at the closest position on either side. Both hemifields had two letters, a T and an L, upright or inverted, in a given color at a fixed distance of 3 positions around the imaginary circle, as illustrated in Figure 1A. Every position on the imaginary circle could hold one of the colored letters with the exception of the 4 positions closest to the vertical midline. Both colored letters in the same hemifield shared the same color, either green (x=.278, y=.460, Y=14.6 cd/m^2) or yellow (x=.429, y=.479, Y=13.7

cd/m^2(corrected to 14.3 cd/m^2)[1]), which determined the side of the eventual target. Additional grey (x=.316, y=.331, Y=14.4 cd/m^2) sideway T letters (leaning on their right or left side randomly) were added on each hemifield depending on the condition. There was either no additional grey distractors, two distractors between the colored letters, two distractors immediately outside the color letters on the imaginary circle, or four additional distractors two inside and two outside, the colored letters.

EEG recordings and analysis.

The electroencephalogram (EEG) was recorded with 64 active scalp Ag/AgCl electrodes (BioSemi ActiveTwo system) mounted on an elastic cap. Positioning and naming of the electrodes followed the International 10–10 System (Sharbrough, Chatrian, Lesser, Lüders, Nuwer, & Picton, 1991). Data were digitized at a sampling rate of 256 Hz, low-pass filtered online at 67 Hz, and band-pass filtered offline between 0.01 and 30 Hz in post-recording analyses. Trials that received a correct response were segmented, time-locked to the onset of each search frame, from 200 ms prior to display onset to 800 ms after (for a total of 1000 ms). These segments were averaged and baseline corrected based on the mean activity during the 200 ms pre-stimulus period for each experimental condition. The horizontal oculogram (HEOG) was recorded and computed as the difference between signals at two additional electrodes located on the external canthi of each eye. The vertical oculogram (VEOG) was recorded and computed as the difference between signals at an electrode located above (Fp1) and an additional electrode below the left eye. Two additional electrodes were used to record signals at the left and right mastoids, and all signals were re-referenced in post-recording analysis to the average of the voltage at the mastoids. Frames with blinks were rejected based on VEOG variations of more than 50 µV in a 150 ms time-window scrolled throughout each trial segment duration. Frames with horizontal eye movements, defined as HEOG variations larger than 35 µV in a 200 ms time-window scrolled through each trial segment, were rejected.

1 Due to a programming error the yellow initial luminance value was slightly lower than for green or grey, but this was fixed during the course of the testing. Post hoc analyses showed that these small luminance variations did not significantly affect the results.

HEOG and VEOG threshold rejections were adapted from Luck (2005). We verified that each participants residual eye movement toward the target was less than 0.25° of visual angle (less than an average 4 μV residual HEOG amplitude between 300ms and 400ms)[2]. On average, participants moved their eyes less than 0.1° of visual angle toward the target. In order to retain sufficient data by participant, we rejected data from participants who had less than 40% of the frames retained after removing trials (all 6 frames) with incorrect responses and frames with blinks or eye movements. We also rejected participants who had less than 60 frames left in a condition in order to maintain a good ratio signal-to-noise.

Component measures were performed at electrodes of interest for each component: for the N2pc and Ptc at electrode pair PO7/PO8, and for the P3, at CPz. Component amplitude measures for statistical analysis were obtained by averaging the time-point measurements in a window centered on the peak amplitude of the grand averaged waveform across participants at electrodes of interest. The width of the averaging period was set to 60 ms for the N2pc and Ptc components to provide sufficient time points to reduce variance while preventing overlapping the measures of the components. Tests were performed on average amplitude using repeated measure ANOVA with type II error terms. When doing pairwise comparison to detail effects, we used Bonferroni corrections to compensate for false positives.

Due to the unusual aspect of the Ptc component, we measured its latency by calculating what we will refer to as Ptc proxy from now on. The Ptc proxy is calculated by subtracting from each condition with grey distractors the condition with No distractor. The resulting ERL represents the change in activity caused by the addition of grey distractors from our baseline condition (which had no grey distractors). The latency statistics on the N2pc and Ptc were evaluated using the jackknife technique. The jackknife method is based on the computation of

2 Out of the 72 participants for both experiments, 3 participants had average HEOG larger than 4 μV. We examined the results excluding their data and it did not change the observed patterns of results or conclusions, and so we included them in the final results.

N jackknife grand averages where each average is based on N-1 participants, taking out each participant out of one of the averages. The latency at which the component in each of these jackknife grand average waveforms reached a relative amplitude compared to the peak was measured and submitted to an ANOVA corrected by dividing the calculated F by $(N-1)^2$ to correct for the reduced error variance of estimated values (Kiesel, Miller, Jolicœur, & Brisson, 2008; Ulrich & Miller, 2001). To counteract possible confound between component amplitude variations and latency effects, we used a relative amplitude threshold for the jackknife measurements (Kiesel, Miller, Jolicœur, & Brisson, 2008) which corrects for the amplitude variation. The relative threshold amplitude used for the latency measure was 50% of the peak amplitude for the N2pc, the Ptc proxy, and for the P3.

Results.

Behavior.

Given the task structure, with multiple search frames belonging to different conditions in each trial, it was impossible to associate a success or a response time to a specific experimental condition other than target color, which was a between participant factor.

Accuracy data was tested for target color using a repeated measure ANOVA. We found that the proportion of correct responses was greater for yellow targets than for green (My = . 85, SDy = .07; Mg = .79, SDg =.09; $F(1, 40) = 6.72$, $p < .013$).

ERP/ERL.

Following initial analyses of the ERL results, shown in Figure 2A and 2B, we determined that despite our efforts to equate both the luminance and the distance in the CIELUV color space across the 3 colors in the experiment (yellow, green, and grey), which

should make the visual stimuli perceptually equivalents, we failed to prevent color effects and interactions from emerging in the results. These effects, while partly unforeseen, help provide a clearer portrait of the attentional mechanisms during our task.

<<< INSERT FIGURE 2 HERE >>>

Despite the color having an impact on the attentional processing, the overall portrait remained essentially the same across the board. The N2pc amplitude during the time window between 220 ms and 280 ms, tested with a repeated measure ANOVA using factors Color (yellow vs. green) X Distractors (No, In, Out, or In/Out), revealed a main effect of Color ($F(1, 40) = 4.09$, $p < .05$) and Distractors ($F(3, 120) = 5.71$, $p < .0011$) as well as a Color X Distractors interaction ($F(3, 120) = 6.48$, $p < .0005$). In Table 1 we listed the average N2pc amplitude for each Color and Distractor condition. We see from Figure 2A, 2B, and from the N2pc average amplitude measures in Table 1 that the interaction can be understood as a change in the relative amplitudes of the conditions with distractors relative ti the No condition. While the No condition N2pc had about the same amplitude for yellow or green targets, for the yellow-target condition the No distractor condition had the smallest N2pc amplitude relative to the other distractor conditions whereas for the green-target condition the No distractor condition had the largest N2pc amplitude relative to the other distractor conditions. Removing the No condition from the ANOVA both removes the interaction *(*$F(2, 80) = 0.43$, $p > .6$) and reinforces the Color *(*$F(1, 40) = 7.34$, $p < .01$) as well as the Distractors ($F(2, 80) = 8.38$, $p < .0006$) main effects. N2pc amplitude for the No condition is the same across target color ($F(1, 40) = 0.07$, $p > .7$). This pattern is consistent with the notion of a discriminability imbalance between each target color and grey, and hence it appeared only when grey distractors were added to the search array. When no grey distractors were present, green and yellow targets had similar N2pc waves. Once we introduced grey distractors, the green target conditions had clearly smaller N2pc amplitudes than the yellow target conditions. When combining target-color conditions to understand effects of distractors when we take out the No condition (and the color interaction), pairwise comparisons showed that adding distractors only between (Inside) the target color items ($t(41) = 2.84$, $p_{corrected} < .03$) or paired with distractors outside (In/Out) ($t(41) = 3.47$, $p_{corrected} < .004$) led to a smaller N2pc compared to the condition where

distractors are only outside the color items. We also performed pairwise comparisons across distractor condition within each color condition. The N2pc was larger in the No condition than in the In/Out condition ($t(20) = 3.76$, $p_{corrected} < .008$) for the green targets. For yellow targets, the N2pc was smaller for condition No ($t(20) = 4.33$, $p_{corrected} < .002$) and In ($t(20) = 3.02$, $p_{corrected} < .05$) than for the condition Out.

<<< INSERT TABLE 1 HERE >>>

Now consider the onset latency of the N2pc. Recall that statistical tests were based on jackknife averages, which we explained in the EEG analysis section. As can be seen in Figures 2A and 2B, there were differences in onset latency across conditions. An ANOVA using factors Color X Distractors showed a main effect of Distractors ($F(3, 120) = 10.59$, $p < .00001$) as well as an interaction between Color and Distractors ($F(3, 120) = 6.87$, $p < .0003$). The color main effect failed to reach significance ($F(1, 40) = 2.78$, $p > .1$). Pairwise comparisons by target color reveals green targets conditions without grey distractors ($t(20) = 8.17$, $p_{corrected} < .00001$) or with distractors outside ($t(20) = 7.98$, $p_{corrected} < .00001$) had shorter N2pc onset latencies than condition with grey distractors inside and outside. Other green target distractor conditions were not different ($ts < 1.92$, $p > .4$) as well as all yellow target distractor conditions ($ts < 1.96$, $p > .3$).

During the N2pc time-range, the perturbation of attentional deployment by the distractors between (Inside) the two target-color items led to a decrease in component amplitude. This is consistent with the vision of the N2pc as an indicator of a successful selection and individuation of a target. A productive but effortful attentional deployment leading to a larger N2pc, while sub-optimal deployment performance lead to a decrease in N2pc amplitude. Also, increased difficulty to discriminate green targets from the grey distractors appears to have introduced a delay in the N2pc onset for the condition with grey distractors both inside and outside. Variability in the condition with distractors only inside seem to be responsible for preventing this condition from showing a latency effect.

While the foregoing results give us an idea of the effect of the distractors on the deployment of attention, the inclusion of the deflection following the N2pc, known as the Ptc, which is also the time-range of a component purportedly related to the inhibition of distractors, the Pd (Hickey, Di Lollo, & McDonald, 2009; Sawaki, Geng, & Luck, 2012; Fortier-Gauthier, Dell'Acqua, & Jolicœur, 2013), could help us get a clearer picture. For ease of discourse, we refer to activity in a window from 290 to 350 ms as the Ptc (positivity temporal contralateral; Hilimire, Mounts, Parks, & Corballis, 2009).

The Ptc mean amplitudes (see Figure 2A, 2B, and Table 2), were dominated by a main effect of Distractors ($F(3, 120) = 21.65$, $p < .00001$) when tested with a repeated measure ANOVA using factors Color X Distractors. There were no other effects, all Fs < 0.8, ps > .05. We examined the effects of Distractors using pairwise comparisons. These tests showed that all conditions with distractors were significantly different from the condition without grey distractors (all $p_{corrected} < .0005$). No other pair of distractor condition reached significance (ts < 2.49, ps > .1). The unusual shape of the Ptc, particularly for the green-target condition, made it difficult to estimate the latency of the Ptc using the same approach for both color conditions.

<<< INSERT TABLE 2 HERE >>>

In order to explore lateralized activity further in this time range, we subtracted from each condition with grey distractors the condition with No distractor, making it a *de facto* baseline. These subtractions we call Ptc proxy are shown in Figure 3A and 3B. We then estimated the latency of the negative component, obtained using 50% of peak amplitude as threshold for jackknife averages tested with an ANOVA using factors Color X Distractors. The analysis revealed main effects of Color ($F(1, 40) = 25.72$, $p < .00001$) ($M_g = 294.9$ ms, $SD_g = 35.3$, $M_y = 257.3$ ms, $SD_y = 36.8$) and Distractors ($F(2, 80) = 21.62$, $p < .00001$), and an interaction between Color and Distractor ($F(2, 80) = 17.37$, $p < .00001$). Mean latencies can be seen in Table 2. Pairwise comparisons reveals that the Ptc proxy negative component had no latency effect between distractor conditions for green targets (ts < 0.8, ps > .9), but for yellow targets the Out condition had a shorter latency than both In ($t(20) = 7.38$, $p_{corrected} <$.

00001) and In/Out ($t(20) = 6.44$, $p_{corrected} < .00001$) conditions. Latencies for yellow targets In and In/Out conditions were not different ($t(20) = 0.68$, $p_{corrected} > .9$). The latency delay on the calculated Ptc proxy was likely to represent the increased negative amplitude of the Out distractor condition compared to the No and In conditions during the N2pc time-window for yellow targets. We see in Figure 3A and 3B, the activity difference between distractor conditions started earlier and lasted longer for yellow targets than for green targets during (and even before) the N2pc time-window.

<<< INSERT FIGURE 3 HERE >>>

Despite differences seen in Figure 3A and 3B, the addition of the grey distractors to the No condition produces very similar results across the two Color condition. The resulting peaks are more well-defined in time than one could expect from the apparent component jitter that was evident in Figure 2. An increased smearing of activity with more distractors could be expected to appear as smaller amplitudes spread over a longer period of time or increasing peak amplitude latency with a more difficult task. Instead, we saw an increase of amplitude with additional distractors at a specific time, the waveform inflection that followed the N2pc, namely the Ptc (see Figure 3). Also, the time-window corresponding to the N2pc had the opposite pattern of amplitude as this negative component. In fact, when we go back to our N2pc lateralization and we test the time-window including both components (220 ms to 350 ms), with a repeated measure ANOVA using factors Color X Distractors, we observed a main effect of Distractors ($F(3, 120) = 6.11$, $p < .0007$) and an interaction between Color and Distractor ($F(3, 120) = 2.74$, $p < .05$). Looking at pairwise comparisons as a reference, we saw the condition without distractors for yellow targets was different from the 3 conditions with grey distractors (Out : $t(20) = 3.88$, $p < .006$; In : $t(20) = 4.30$, $p < .003$; In/Out : $t(20) = 4.29$, $p < .003$), the No condition amplitude being less negative than the conditions Out, In, and In/Out, which were not different from each others (ts < 0.6, $p > .9$). For green targets, all conditions were equivalent (ts < 1.1, $p > .9$). This suggests a delay, or spillover, of activity caused by adding distractors that produces interference between the N2pc time-window and another peak in the time-window of the Ptc. With increasing difficulty to individuate the target

from the surrounding, the activity that normally happens during the N2pc time-window appears to be pushed to a subsequent time-window.

In order to provide converging evidence concerning the impact of these distractors on mechanisms of attention, we performed analyses focusing on the P3 component. The P3 is believed to reflect, at least in part, mechanisms that update working memory with representations that are used in producing controlled responses and verbal reports (Donchin, 1981; Vogel, Luck, & Shapiro, 1998). The latency of the P3 can be used as an indicator of stimulus evaluation sensitive to sensory and cognitive demands of the task (Dell'Acqua, Dux, Wyble, Doro, Sessa, Meconi, & Jolicoeur, 2015; Ptito, Arnell, Jolicoeur, & MacLeod, 2008; Verleger, 1997). As such, the P3, provides us with a powerful tool to evaluate the differential processing demands of the distractor conditions. Our experimental paradigm, which has an equal number of trial with 3, 4, 5, or 6 frames with a target (target color Inverted T) implying more frames with a target than without, did not present the typical ratio between target and non-targets to elicit a novelty P3. However, we asked participants to add to an internal count whenever they saw a target, which would be consistent with a view of the P3 as a context-dependent update of the working memory used to maintain the internal count (Donchin, 1981; Donchin & Coles, 1986).

For each distractor condition, we computed new ERPs that averaged frames that contained a target (target-present) and those that did not (target-absent). We then subtracted target-absent from target-present ERPs to isolate the P3 response specifically related to target processing, for each distractor condition (ignoring target side). Figure 4A presents the resulting grand average waveforms at electrode CPz, in the region of maximum amplitude of the scalp distribution of the difference component. The onset latency effect on the P3 difference waveform was tested with a repeated measure ANOVA using factors Color X Distractors based on jackknife estimates of component latency and only revealed a Distractors main effect ($F(3, 120) = 17.06$, $p < .00001$). There was no Color main effect ($F(1, 40) = 1.82$,

$p > .18$). Pairwise comparisons indicated a shorter P3 latency for the No condition (M_{no} = 378.2 ms, SD_{no} = 35.5) compared to all other distractor conditions (M_{out} = 401.7 ms, SD_{out} = 47.4, $t(41) = 3.18$, $p_{corrected} < .02$; M_{in} = 401.4 ms, SD_{in} = 35, $t(41) = 3.27$, $p_{corrected} < .02$; $M_{in/out}$ = 428.1 ms, $SD_{in/out}$ = 37.3, $t(41) = 8.19$, $p_{corrected} < .00001$). Both Out ($t(41) = 3.9$, $p_{corrected} < .003$) and In ($t(41) = 3.79$, $p_{corrected} < .003$) conditions had also shorter latencies for their respective P3 than the In/Out condition, but they were not different ($t(41) = 0.37$, $p_{corrected} > .9$) from each other.

<<< INSERT FIGURE 4 HERE >>>

We can observe that across nearly all tests performed the trend was consistent with an increasing task demand from the No condition to the Out and In conditions (which were similar) and finally the In/Out condition, which was the most difficult.

Discussion.

Grey distractors are parts of many visual search experiments used to study the n2pc, and often they are not considered explicitly when they are balanced between hemifields. The results we present here suggest that grey distractors can provoke important alterations to the timecourse of attentional processing reflected in the N2pc component.

There were a number of notable more specific results from Experiment 1. Firstly, for yellow targets, we observed increases in N2pc amplitude for conditions where grey distractors were added. This is consistent with an increased attentional processing required to individuate the target from the surrounding grey distractors, although the largest increase was not from the condition with the most distractors. One explanation for the larger N2pc for distractors outside compared to the conditions with distractors inside could be that attentional processing in those conditions was not as effective. Another explanation that we favor takes into account the following time window, of the Ptc. The Ptc time window displays the inverse pattern of amplitudes compared to the N2pc window for the conditions with grey distractors. The

amplitude of both time-windows combined showed no amplitude differences between distractor conditions. This leads us to believe that the effect of grey distractors was spread across the N2pc and Ptc time-windows in a systematic manner. More difficult processing of the target (or increase in distractor interference) pushed a larger portion of the activity from to the N2pc time window into the Ptc time window, thus reducing the apparent amplitude of the N2pc while making the Ptc more negative.

Secondly, the P3, which we use to index working memory updating, is increasingly more delayed with the addition of distractors. This confirms that the addition of grey distractors creates a lasting delay in downstream processing with more distractors leading to longer delays. This also supports the view that the smaller N2pc for distractors inside and outside is not indicative of an easier task, but a symptom of more activity being delayed into the Ptc time window. Variability in this process produced a smeared N2pc, that was particularly apparent for green targets.

Thirdly, conditions with grey distractors for green targets had a smaller N2pc and a more negative Ptc compared to the No condition. The No condition N2pc for green targets was actually statistically equivalent to the No condition N2pc observed for yellow targets. This suggests an interaction between the target color (green) and the distractors used in the task. This color effect is likely related to a weaker discriminability between green and grey compared to yellow and grey. The reduced discriminability relative to the grey distractors would increase the impact of grey distractors in the processing of green targets compared to what we found for yellow targets. This would result in greater smearing of the N2pc into the Ptc time window for green than for yellow targets, as was evident when we compared results across panels A and B of Figure 2.

Experiment 2

The results of Experiment 1 provided clear-cut and striking effects of the addition of low-salience distractors on the temporal dynamics of attention revealed by the N2pc component. We argued above that the color differences in the degree of smearing of the n2pc for green versus yellow targets probably reflected differences in discriminability between each color and the lower-salience grey distractors. Before we accept this conclusion, however, we need to consider an alternative explanation based on potential competition for selection between green and yellow. In Experiment 1, recall that each display had yellow items in one hemifield and green items in the other. It is possible that yellow targets were better at guiding attention to their location than green targets; or that yellow interfered more with green targets than vice versa. Thus, possible differences in the attentional salience of the colors could have created a competition between green and yellow, which may have been exacerbated by the addition of grey distractors.

In order to ensure the non-target display hemifield did not capture attention (or interfere in some other way) differentially for yellow and green distractors, in Experiment 2 we forwent the mirroring intended to balance the color discontinuities between the visual hemifields to ensure the effects observed were not due to competition between salient items across hemifields. Displays in Experiment 2 had no color in the hemifield controlateral to the target, as illustrated in Figure 1B for the yellow-target condition. If competition between salient items across visual hemifields was the cause of differential effects of color in Experiment 1, these effects should be eliminated in Experiment 2.

Method.

Participants.

34 Participants, of which 30 were kept for analysis (12 males, average 21.7 years old), completed the experiment voluntarily and received monetary compensation after providing written informed consent. They had normal or corrected to normal vision, were neurologically

normal, and were not taking neurologically-active medication according to self reports. Four participants were rejected after completing only part of the experiment or a low success rate and/or eye movements during trials led to the elimination of more than 60% of the data. Two participants completed only 5 experimental blocks and another participant completed 4 experimental blocks while still meeting the criteria for inclusion. The experimental paradigm was vetted by the ethics committee of the faculty of arts and science at Université de Montréal.

Procedure.

We used the same procedure as in Experiment 1.

Stimuli.

The stimuli were the same as in Experiment 1 except that only the potential-target items were colored; all other items were grey, as illustrated in Figure 1B. Both target colors and grey were balanced in luminance and CIELUV color space distance to reduce color effects (green, x=.275, y=.464, 14.2 cd/m^2; yellow, x=.415, y=.485, 14.3 cd/m^2; grey, x=.309, y=.328, 14.2 cd/m^2). The resulting display frames had color only in one hemifield.

EEG recordings and analysis.

We performed the same data analysis as in Experiment 1 using ANOVAs with type II error terms. In order to test for possible interactions with Experiment 1 and 2 results, we tested these effects using ANOVAs with type III error terms, adding an Experiment factor to the statistical models.

Also, given more overall data, we performed a linear regression on the accuracy data combined across both experiments to give an indication of the contribution of each condition to accuracy in the task. For each trial, we counted the frames belonging to each distractor condition and used them to predict accuracy. This was achieved using multiple linear regression by entering the counts of Out, In, and In/Out as explanatory variables for the accuracy. Given that most (66) participants performed 576 trials, three participants completed 480 trials, one 385 trials, one 284 trials, and one 577 trials, the regression considered 40802 trials.

Results.

Behavior.

Accuracy data was tested for target color using a between-subjects ANOVA. We found that the proportion of correct responses was greater for yellow targets than for green (My = .88, SDy = .07; Mg = .77, SDg = .1; $F(1, 28) = 10.33$, $p < .004$). We also tested the result of both experiments using factors Color X Experiment model to determine if accuracy levels were affected by the presence/absence of colored items in the hemifield opposite to the target hemifield. No Experiment effect ($F(1, 68) = 0.08$, $p > .7$) or interaction ($F(1, 68) = 0.91$, $p > .3$) could be found. Since no experiment effect was found, in order to understand the accuracy results in more detail, we used regression analyses to predict success in reporting the correct target count in a given trial from the number of frames in each Distractor condition (no additional distractor (No) as baseline, distractors inside (In), distractors outside (Out), distractors inside and outside (In/Out)) in a trial. The regression analysis demonstrated that accuracy could be predicted from a knowledge of the distractor conditions in a trial ($F(3, 40798) = 12.67$, $p < .00001$; adjusted $R^2 = .0009$). Regression analyses provided estimates to determine how each distractor condition contributed to overall success in a trial. Positive estimates would indicate that more frames of a given type predicted better performance whereas negative estimates would indicate that more frames of a given type predicted worse performance. We used the No condition as a baseline, and we obtained estimates for the Out,

In, and In/Out conditions of -0.0054 (t(40798) = 2.36, p < .02), -0.0063 (t(40798) = 2.74, p < .007), and -0.014 (t(40798) = 6.11, p < .00001), respectively. These results indicate that the condition with no additional distractor was more likely to lead to a correct response than all conditions with grey distractors. The estimates indicate that distractors inside and distractors outside condition led to higher accuracy than distractors both inside and outside. The condition with distractors outside was equivalent to the condition with distractors inside in terms of impact on overall accuracy. In general, these results suggest that the addition of distractors made the task more difficult.

ERP/ERL.

As can be seen in Figures 2C and 2D, the lateralized waveforms from Experiment 2 show essentially the same patterns we observed in Experiment 1 (Figure 2A and 2B). We can see the reduced N2pc and more negative Ptc for grey distractor conditions. Also, we can see the clear differences between green and yellow targets in the various waveforms. These general observations were verified by detailed analyses presented in the following paragraphs.

The amplitudes of N2pc for the same time-window as in Experiment 1 (220 ms – 280 ms) for each participant were submitted to a repeated measure ANOVA using factors Color X Distractors and showed no significant effect (Distractors, (F(3, 84) = 2.31, p > .08); Color, (F(1, 28) = 2.65, p > .1); Color X Distractors interaction (F(3, 84) = 1.13, p > .3)). During this time-window, there were no effect of Experiment or interaction with Experiment (Fs < 1.1, ps > .3). When we looked at the waveforms (clearer for green targets), the Distractor effect seemed to occur earlier in Experiment 2 than in Experiment 1, possibly due to the facilitation of the target side selection with the absence of color in the opposite hemifield. For this reason we redid the previous analysis but used mean amplitudes in a slightly earlier time window from 180 ms to 240 ms. In this analysis we found a Distractor main effect (F(3, 84) = 10.35, p < .00001), although the Color main effect (F(1, 28) = 3.47, p > .07) was marginally significant and the Color X Distractors interaction was not significant (F(3, 84) = 0.99, p > .4). In Table 1

we listed the average N2pc amplitudes for each Color and Distractor condition for the same time-window as in Experiment 1. We performed pairwise comparisons across grey distractor conditions for the 180 ms – 240 ms time-window leaving the No condition aside (M_{no} = -0.52, SD_{no} = 0.6). The time-window activity in the Out condition (M_{out} = -0.68, SD_{out} = 0.89) and in the In condition (M_{in} = -0.43, SD_{in} = 0.76) were more negative (Out, $t(29) = 4.74$, $p_{corrected} < .0002$; In, $t(29) = 3.16$, $p_{corrected} < .02$) than the In/Out condition ($M_{in/out}$ = -0.09, $SD_{in/out}$ = 0.87). The Out and In conditions were marginally different ($t(29) = 2.47$, $p_{corrected} < .06$).

The N2pc onset latency was tested as in Experiment 1 using jackknife estimates followed by a repeated measure ANOVA using factors Color X Distractors. We found a main effect of Distractors ($F(3, 84) = 6.53$, $p < .0006$), without Color main effect ($F(1, 28) = 1.23$, $p > .2$)) or Color X Distractors interaction ($F(3, 84) = 1.58$, $p > .2$)). N2pc onset latencies by condition of target color and distractor are reported in Table 1. When including Experiment 1 data, there were no significant Experiment effect or interactions (Fs < 1.7, ps > .1). Pairwise comparisons showed a longer latency for the grey distractor inside and outside compared to the condition with no distractors ($t(29) = 2.86$, $p_{corrected} < .05$) and the condition with distractors outside ($t(29) = 3.28$, $p_{corrected} < .02$).

The Ptc mean amplitudes (see Figure 2C, 2D, and Table 2) had a main effect of Distractors ($F(3, 84) = 18.59$, $p < .00001$) when tested by a repeated measure ANOVA using factors Color X Distractors. There were no other significant effects in this ANOVA, all Fs < 0.6, ps > .6. When including Experiment 1 data, there was no significant Experiment effect or interactions (Fs < 1.3, ps > .2). We examined the Distractor main effect using pairwise comparisons which showed that all pairs of conditions were significantly different (ts > 2.86, ps < .05) except for the difference between the In and Out conditions ($t(29) = 0.18$, $p_{corrected} > .9$).

We extracted a Ptc proxy similar to Experiment 1 by using the No condition as a baseline for all conditions with grey distractors (see Figure 3C and 3D). The onset latency of the negative component of the Ptc proxy tested with an ANOVA using factors Color X Distractors revealed main effects of Color ($F(1, 28) = 5.21$, $p < .04$) and Distractors ($F(2, 56) = 10.87$, $p < .0002$), but no interaction between Color and Distractor ($F(2, 56) = 2.33$, $p > .1$) (see Table 2 for mean latencies). When including Experiment 1 data, there were no significant Experiment effect or interactions (Fs < 0.4, ps > .5). The Ptc proxy negative component onset latency was slower for green targets than for yellow targets. Pairwise comparison showed the Out distractor condition to have shorter latency than both the In distractor ($t(29) = 3.7$, $p_{corrected} < .003$) and the In/Out distractor ($t(29) = 3$, $p_{corrected} < .02$) conditions. The In and In/Out conditions were not different ($t(29) = 1.65$, $p_{corrected} > .3$).

The onset latency on the P3 difference waveform was tested with repeated measure ANOVA using factors Color X Distractors based on jackknife estimates revealed no significant effect (Color, $F(1, 28) = 0.06$, $p > .8$; Distractors, $F(3, 84) = 1.53$, $p > .2$; Color X Distractors, $F(3, 84) = 0.19$, $p > .8$). When including Experiment 1 data, there was no significant experiment effect or interactions (Fs < 0.8, ps > .5), but the overall Distractor effect was still significant ($F(3, 204) = 8.64$, $p < .00002$).

Discussion.

The removal of the color from one side of the search array stimuli did not change the most important patterns of results across distractor conditions and target-color conditions relative to what was found in Experiment 1. Globally, we still observed a smaller N2pc amplitude for the Out condition than In and In/Out conditions (when using a slightly earlier window than in Experiment 1). The absence of competing color could have accelerated the target selection process slightly, particularly for green targets, but otherwise did not change the impact of adding grey distractors to the search displays.

We performed Experiment 2 to verify if a competition for selection between the two target colors could be responsible for the differences in the ERL for yellow and green targets. Despite the N2pc and Ptc amplitude color effects no longer significant, and the N2pc latency Color X Distractors interaction as well, we did not find any Experiment interaction indicating that the manipulation reduced the differences between target colors. Besides, the Ptc proxy color latency effect remained, showing activity was reduced for a longer period during N2pc time-window for green target than yellow target and the spill into Ptc time-window was steeper. The distractor effect, as can be seen on Figure 3 ERLs subtractions, was very similar across the two experiments. The clearest change in the subtraction proxy was an earlier positive peak for green targets in Experiment 2, which is more similar to the yellow target latency. This suggest the initial individuation of the target from grey distractors started earlier for green targets when we removed competition with yellow, but the color differences in the dynamics of activity spill from the N2pc time window to the Ptc time window was largely unaffected. Overall, when looking at the subtraction waves shown in Figure 3 (subtracting the activity in the No distractor condition from that of the other conditions), the patterns of activity propagation into the Ptc time window were very similar across target colors and experiments. The timecourses were slightly different but the general patterns were the same. We found no effect or interaction of Experiment for any measure in the analyses we performed.

The absence of significant P3 latency effects in Experiment 2 were likely due to insufficient power because the patterns were similar to those observed in Experiment 1, which were significant (see Figure 4). The supplemental regression analysis we performed for the accuracy results in combined data from both experiments strenghten our confidence in the P3 pattern suggesting that more grey distractors make the task more difficult, leading to lower accuracy the more grey distractors are present in the stimulus.

General Discussion

The primary intent of our study was to discover the impact of less salient distractors on attentional mechanisms that mediate processing of salient and task-relevant stimuli. We examined modulations of attentional processing for distractors inside, outside, or both inside and outside, an "area of interest" created by salient task-relevant stimuli. The "focus of attention" was more likely to include distractors surrounding potential targets if the target could not be extracted pre-attentively via a single feature. In our paradigm, the non-target letter (L) in the target color was sufficient to help orient initial attentional deployment toward the area containing the colored items, while being sufficiently similar to the target not to be rejected preattentively (Luck & Hillyard, 1994). Participants had to contend with that significant distractor while performing the search task leading to an attentional deployment that was not as focused and centered around the target as a "pop out" search would normally generate. The overall pattern that emerged from the addition of grey distractors near the target was one of increasing difficulty to individuate the target related to the number of distractors and to their position in relation to the "area of interest". This view was supported by an increasing attentional deployment delay as well as a delayed P3, and lower accuracy, as we increased the number of grey distractors.

The observed effects of the grey distractors manipulation on the N2pc, which is an index of attentional deployment, suggest that the grey distractors disrupt attentional deployment. N2pc amplitude was smaller for distractors inside compared to outside the "area of interest." We also found (Figure 2) that distractors modulated the amplitude of N2pc both positively and negatively. Our understanding of this apparent non-linear effect is that the increase in attentional processing caused by the distractors is spread across the time-windows of the N2pc and Ptc. The additional processing is similar for all 3 conditions with grey distractors (In, Out, and In/Out), the increased activity being an increased effort to individuate the target from the distractors. The differences between conditions reside in the proportion of activity that occurs within the N2pc time-window compared to activity that is delayed and appears in the Ptc time window. This delay, and likely the variance in the delay across trials

and subjects, increases with increasing disruption from distractors. The condition with distractors outside shows the least disruption with most activity remaining in the N2pc time-window while both conditions with distractors inside have a reduced N2pc and a more negative Ptc. The condition without additional distractor appears to provide a reliable baseline measure of the attentional deployment waveform when no additional distractor were present. The lack of increase or even the reduction of the amplitude of the N2pc has been interpreted previously as a failure to individuate a potential target despite an increased task demand for individuation (Bacigalupo & Luck, 2015). From the results we have here we can suggest that smearing of N2pc activity with increasing uncertainty could explain why an increased need for attention (caused by adding distractors) would lead to the observation of a smaller N2pc (in the usual time window).

We argue that an understanding of the effects of added distractors requires taking into account a longer window, extending beyond the usual N2pc component window, into what we call here the Ptc time-range (290 – 350 ms). The Ptc has been proposed by Hilimire et al. (2009) as a distractor inhibition component and revised by Hilimire et al. (2014) as more likely linked to the end of attentional deployment. The Ptc is typically a return of the contralateral negative waveform towards baseline accompanied with an occasional overshoot into the positive. We tend to view this component more as a landmark time-range following the N2pc than as a clear component indexing a positive process, which is most clearly visible here in the No condition (see Figure 2). When we consider the ERLs observed when we added grey distractors to the display, the Ptc time-range demonstrated an inverted amplitude pattern for the distractor conditions compared to the patterns seen during the N2pc time-range. Additional distractors led to a more negative Ptc. The inversion and the fact that the time-range including both N2pc and Ptc time-ranges shows an equally increased negative amplitude value for all distractor conditions (In, Out, and In/Out) support a view where a single process is smeared across both time-ranges. The increase in distractor interference between conditions would push part of the processing into a subsequent time-window that is usually indicative of the completion of the attentional deployment. The more disruptive effect of the distractors

could be attributed to the distractors inside the “area of interest” as shown by the lower initial N2pc amplitude compared to the amplitude when the distractors were presented outside only. The large component following the Ptc time-window did not seem to be delayed by the distractor manipulation, which could suggest that the distractors attentional disruption was absorbed during the earlier attentional processing. Nonetheless, these earlier disruptions of the attentional mechanisms could be observed in delays of the onset of the P3, as well as in accuracy results. Despite being unable to separate inside and outside distractor effects statistically on most tests, across all amplitude and delay effect there was a trend suggesting more disruption for distractors inside compared to distractors outside of the “area of interest.”

Another important finding was that that the trade-off between N2pc and Ptc time-range activity was contingent on the target color, the number of distractors, and the position of those distractors. The difference ERLs for the distractor conditions compared to the no distractor condition (Figure 3) also revealed that the peak of the delayed activity has little latency variation between each distractor condition. Smeared activity provoked by an increase in individuation difficulty should lead to a delayed activity peak that is increasingly delayed between each distractor condition from the Out, to the In, and to the In/Out condition. Instead, the activity seemed to be more frequenty pushed back with increased difficulty leading to an graded amplitude modulation during the N2pc and Ptc time-window, but the latency by which the activity was pushed back seemed to be similar on average for each distractor condition resulting in similar negative peak latency in the Ptc proxy despite increasing individuation difficulty. This pattern of delayed activity could be indicative of a serial deployment of attention between potential targets, given our search included two potential targets, rather than a delay applied to a single deployment of attention toward the target. With increased disruption from distractors, the target could be harder to select without attentional processing and an initial erroneous deployment could happen in a subset of the frames to help select the correct target. The various factors that impact attentional deployment in our task (colour, position, number of distractors) all seem to contribute to that same mechanism of attentional compensation. The more difficult those factors caused the initial individuation of the target to

be, the larger proportion of the activity is pushed from the N2pc to the Ptc time-window or the more probable it is to provoke an erroneous initial attentional deployment (i.e., deployment to the salient L distractor).

As in previous work, we found significant differences across colors used to designate targets (e.g., Fortier-Gauthier, Dell'Acqua, & Jolicœur, 2013). Although the green target waveforms demonstrated the same general trends as for the yellow targets, there were a number of interesting differences (Figure 2). The recurring main color effect in both experiments when excluding the condition without distractor was a longer latency for the negative component of the Ptc proxy (Figure 3) for the green target compared to yellow target. This could be seen in the ERLs as a “sloppy” N2pc with little or no peak in the usual time window. In Experiment 1, which had balanced color discontinuities across hemifields, there was a smaller N2pc and a more negative Ptc for green targets. In Experiment 2, where we removed the potentially-competing color in the non-target hemifield, the appearance of the green ERLs was very similar to what was seen in Experiment 1, but if anything, we found earlier effects of the grey distractors for green targets relative to those found for the yellow targets (Figure 3C and 3D). Perhaps removing color from the other side of the display was why the disruptive effect of the grey distractors for green targets occured earlier, partially out of the time-window of the N2pc comparatively to the yellow activity which remained largely unchanged. These patterns suggest the competing effect for attention selection of green and yellow items delayed the individuation process for green target, aligning it with the N2pc latency. Removing inter-hemifield competition, thus facilitating the selection, removed the onset latency difference across target colors. Given that target-color differences remained in the absence of inter-hemifield competition, we suppose that such competition was not the principal cause of color effects. Thus, the results are more consistent with explanations in terms of a contrast or salience imbalance between green targets and the grey distractors relative to the contrast or salience for yellow against grey. Green has already been reported as less likely to capture attention compared to other colors (Ansorge & Becker, 2014; Fortier-Gauthier, Dell'Acqua & Jolicœur, 2013; Jetté Pomerleau, Fortier-Gauthier, Corriveau,

Dell'Acqua, & Jolicœur, 2014) even when color space distances between green or yellow and grey were equivalent. Without additional distractors, both colors produce similar ERP waveforms when performing a search task against a dark background. In the presence of distractors, however, we need to consider how well they stand out from them. The green targets led overall to lower accuracy than yellow targets and Experiment 2, with a single side having colored items, did not produce markedly different results compared with Experiment 1 (green on one side and yellow on the other) as attest the absence of Experiment factor effects. This suggests that ERLs differences between yellow and green were driven partly by competition but that color discrimination between green and grey are likely responsible for the accuracy and timecourse differences between the N2pc and Ptc. A previous pilot experiment with the same general task but with grey targets and green distractors showed the same trend of increased delay, which would tend to designate the color contrast as an important factor. Compounding the additional distractors and the increased in discrimination difficulty led to a larger proportion of delayed N2pc trials for green targets than for yellow, but when the contrast was removed by removing the grey distractors, the two colors showed similar results. Thus, the difficulty to individuate the target from distractors is an important source of attentional deployment delay during our search task, and that distractor numerosity and position as well as color are all contributing factors.

The source of the disruption caused by the addition of grey distractor to the search array is still uncertain. The crowding effect impact on the N2pc could be part of the explanation (Bacigalupo & Luck, 2015). Each position around the circle was within the limit of crowding effect from the next position as noted by Bouma's rule (Whitney & Levi, 2011), which state that for complete visual isolation of an item presented at an eccentricity of φ°, no other item should be present within 0.5 φ° distance of visual angle. Although the color difference should have overcome the crowding effect (Intriligator & Cavanagh, 2001), it is possible the similar array of lines forming the letters could have been affected by crowding nevertheless. Another possible explanation for the effect of grey distractor is the modification of the search display geometry between the different conditions, which could have elicited

slightly different search strategies. Conditions including grey distractor inside the “area of interest” formed a more unified (contiguous) display, whereas the condition without grey distractor inside could be more readily seen as two separate entities. Another possibility is that attention is deployed more broadly as more distractors are added, leading to a dilution of processing. But, this notion seems at odds with the larger impact of the Inside condition in some cases. A similar conclusion was proposed by Heinze *et al.* (1994) with a different experimental paradigm where participant were asked to attend to two items and distractor onsets between them generated a larger P1 than distractor onsets outside the region spanned by them. Although, our results do not allow for a definitive conclusion in this matter, the addition of grey distractors did disrupt attentional deployment, which indicates that attention could not be tightly focused on just the two potential targets in the target color.

In conclusion, adding proximal form distractors delays the onset of attentional engagement. This is reflected in the results as a smearing of the N2pc into the subsequent window (Ptc). This is more easily seen for green targets than for yellow targets (Figure 2), because the degree of slowing is larger for green targets. Otherwise, the impact of proximal distractors is quite similar across target colors, which can be seen when we compare conditions with distractors against the no-distractor condition more carefully, as shown in Figure 3. These attentional delays propagate to memory encoding (P3) and ultimately to observable behavior (accuracy). It is clear that the grey distractors in circular displays populated by colored probable targets and distractors cannot be ignored by the attention system, and so they should not be ignored by researchers who use such displays. The grey distractors may have eluded our attention, as ogres do, but their presence leaves traces we can no longer ignore.

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Figure captions

Figure 1. A) Exemples of each balanced distractor condition. While the two potential targets were at fixed distance on the perimeter of an imaginary circle there was either (from left to right), no additional distractor, two grey distractors between the two potential targets, two distractors just outside the area delimited by the potential targets or 4 additional grey distractors inside and outside. B) Exemples of each control distractor condition. This version of the experiment was used to ensure the observed effect were not due to competition between target and distractor colors. C) The 6 search arrays were presented on multiple successive frames separated by jittered-duration fixation screens. The count of targets found which could range from 3 to 6 was to be delivered after the last frame was presented.

Figure 2. Grand average ERLs for each distractor condition at electrode pair PO7/PO8 for A), C) yellow target and B), D) green target. Experiment 1 ERLs are presented in the top row and experiment 2 ERLs are presented on the bottom row. For conditions with grey distractors (In, Out, In/Out), we can see during the N2pc time window (220–280 ms) a more negative component for distractors outside compared to distractors inside and inside and outside. The relative amplitudes across conditions changes during the Ptc time window (290–350 ms) where distractors both inside and outside (In/Out) are most negative compared to distractors inside (In) or outside (Out) only.

Figure 3. ERLs subtractions of the no distractor condition from each condition with grey distractors at electrode pair PO7/PO8 for A), C) yellow target and B), D) green target. Experiment 1 ERLs are presented in the top row and experiment 2 ERLs are presented on the

bottom row. We used this waveform calculation to test latency effects on the Ptc as well as to visualize better the modulations brought by the additional grey distractors. We see the high similarity across color conditions (left vs. right pannels) in terms of the impact of grey distractors. Note the earlier onset latency of the separation between distractor conditions in the experiment 2 spilling out of the N2pc time-window.

Figure 4. ERPs for each distractor condition at electrode site Cpz. A) The experiment 1 and B) experiment 2 P3 calculated by subtrating the target-absent ERP from the target-present ERP. They present to the eye a similar pattern of onset latency delay by distractor condition with more distractors leading to longer P3 latencies.

Figure 1

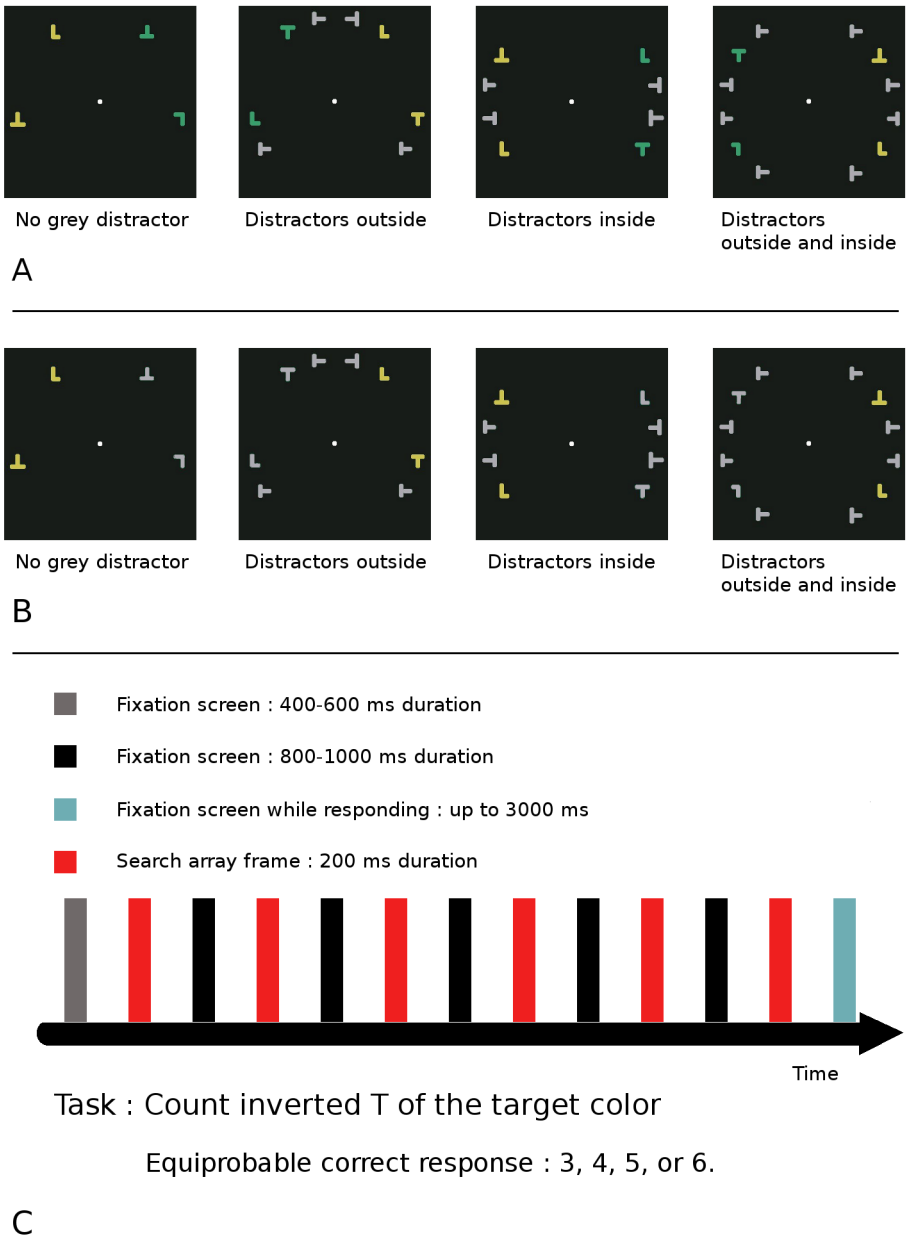

No grey distractor
Distractors outside
Distractors inside
Distractors outside and inside
A
No grey distractor
Distractors outside
Distractors inside
Distractors outside and inside
B
Fixation screen : 400-600 ms duration
Fixation screen : 800-1000 ms duration
Fixation screen while responding : up to 3000 ms
Search array frame : 200 ms duration
Time
Task : Count inverted T of the target color
Equiprobable correct response : 3, 4, 5, or 6.
C

Figure 2

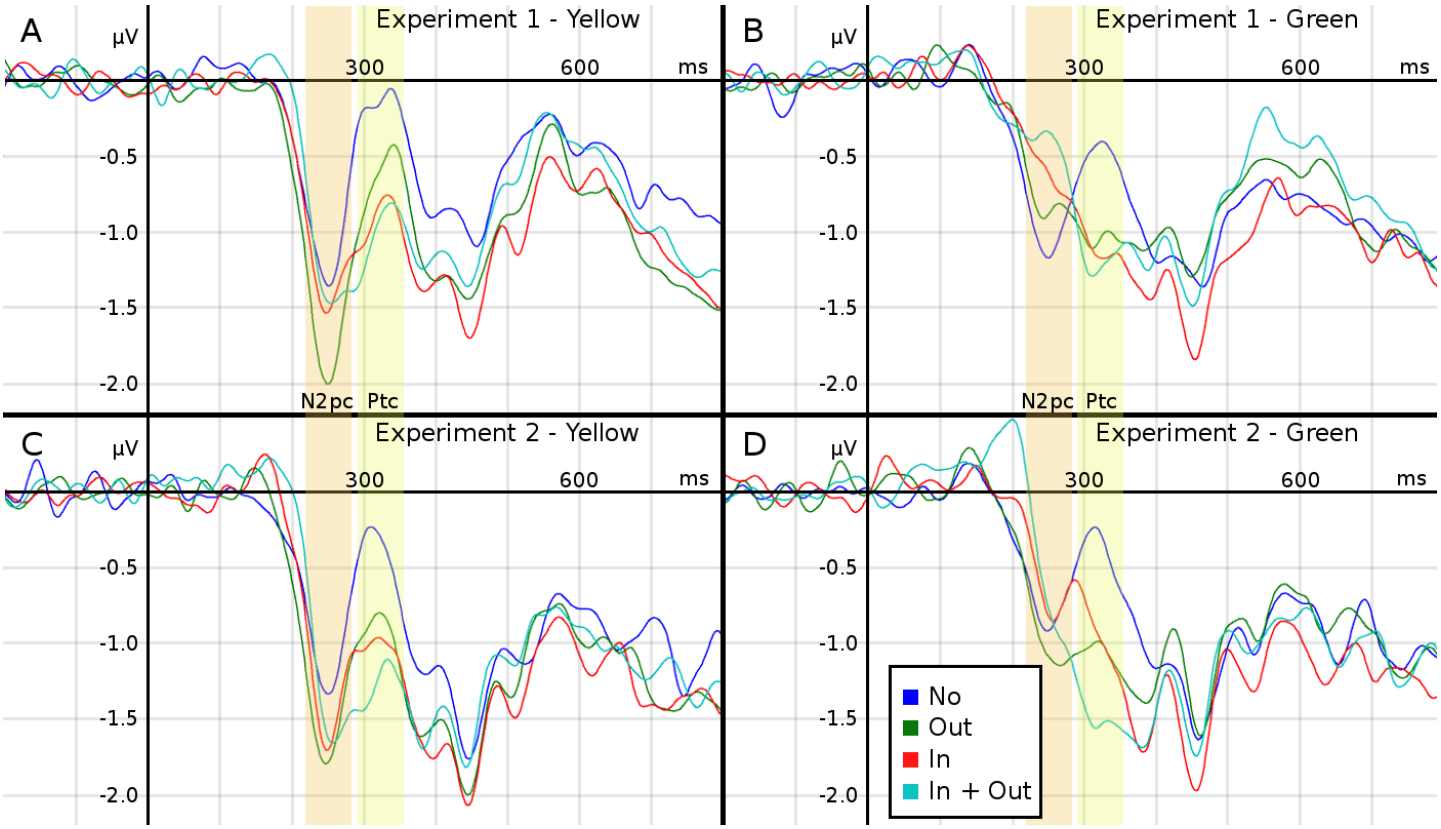

A
Experiment 1 - Yellow
B
Experiment 1 - Green
C
Experiment 2 - Yellow
D
Experiment 2 - Green
µV
300
600
ms
-0.5
-1.0
-1.5
-2.0
N2pc
Ptc
No
Out
In
In + Out

Figure 3

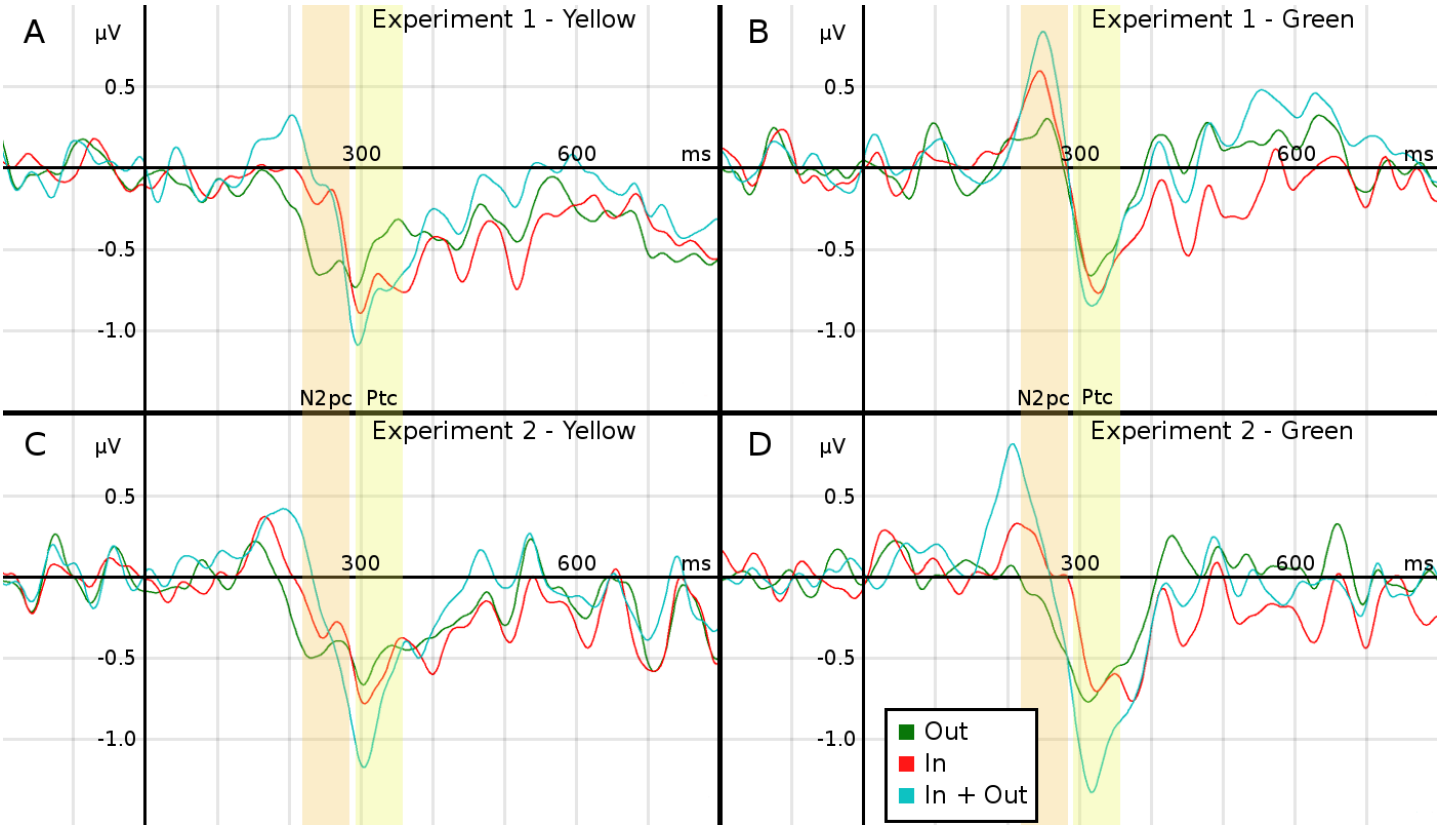
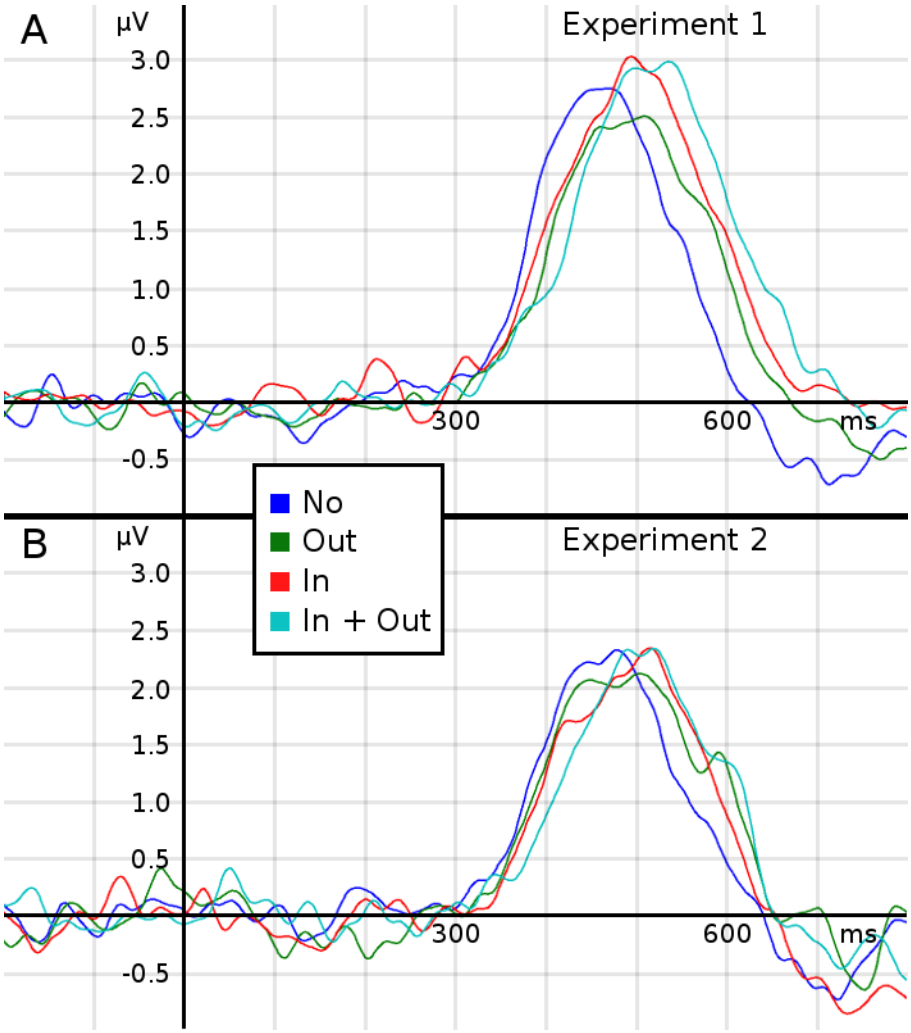

A
μV
Experiment 1 - Yellow
0.5
300
600
ms
-0.5
-1.0
N2pc
Ptc
B
μV
Experiment 1 - Green
0.5
300
600
ms
-0.5
-1.0
N2pc
Ptc
C
μV
Experiment 2 - Yellow
0.5
300
600
ms
-0.5
-1.0
D
μV
Experiment 2 - Green
0.5
300
600
ms
-0.5
-1.0
Out
In
In + Out

Figure 4


A
μV
Experiment 1
3.0
2.5
2.0
1.5
1.0
0.5
-0.5
300
600
ms
No
Out
In
In + Out
B
μV
Experiment 2
3.0
2.5
2.0
1.5
1.0
0.5
-0.5
300
600
ms

Tables

Table 1. N2pc amplitudes and latencies by target color, distractor and experiment condition.

Color	Distractors	Exp.	N2pc amplitude		N2pc latency	
			Mean (μV)	Standard deviation	Mean (ms)	Standard deviation
Green	No	1	-1.02	1.39	213	52.2
Green	Out	1	-0.83	1.2	214.8	46.5
Green	In	1	-0.61	1.01	247.8	115.1
Green	In/Out	1	-0.41	0.96	278.9	41.2
Yellow	No	1	-1.12	1.09	213.7	26.1
Yellow	Out	1	-1.71	1.14	214.6	20.9
Yellow	In	1	-1.32	1.01	215.4	24
Yellow	In/Out	1	-1.3	1.06	221.7	24.6
Green	No	2	-0.78	0.79	216.9	43.7
Green	Out	2	-0.99	0.83	221.6	30.8
Green	In	2	-0.64	0.77	231.8	32.6
Green	In/Out	2	-0.62	0.98	253.6	61
Yellow	No	2	-1.12	0.95	216.2	29.9
Yellow	Out	2	-1.56	1.56	211	33.7
Yellow	In	2	-1.41	1.25	219.3	29.5
Yellow	In/Out	2	-1.38	1.54	226.4	28.7

Table 2. Ptc amplitudes and latencies of the negative component of the Ptc proxy by target color, distractor and experiment condition.

Color	Distractors	Exp.	Ptc amplitude		Ptc proxy latency	
			Mean (μV)	Standard deviation	Mean (ms)	Standard deviation
Green	No	1	-0.5	1.07	—	—
Green	Out	1	-1.03	1	292.9	44.2
Green	In	1	-1.09	0.87	298	37.1
Green	In/Out	1	-1.18	0.9	293.8	22.6
Yellow	No	1	-0.16	1.22	—	—
Yellow	Out	1	-0.66	1.11	219.5	34.6
Yellow	In	1	-0.91	1.21	277.5	20.6
Yellow	In/Out	1	-1.01	1.2	274.9	18.1
Green	No	2	-0.38	0.88	—	—
Green	Out	2	-1.05	0.93	271	87.3
Green	In	2	-0.9	1.09	301.6	30.9
Green	In/Out	2	-1.47	1.02	288.4	24.5
Yellow	No	2	-0.38	0.97	—	—
Yellow	Out	2	-0.91	1.2	209.6	54.3
Yellow	In	2	-1.02	0.79	280.6	55.6
Yellow	In/Out	2	-1.27	0.95	272	45.3

Conclusion

Cette thèse aborde plusieurs aspects de l'attention visuelle. Chacun des chapitres apporte des éléments qui nous permettent de mieux comprendre les mécanismes attentionnels ainsi que l'activité électrophysiologique qui leur est associée.

Le premier chapitre aborde la question de l'activité attentionnelle propre à la cible et au distracteur. En disposant sur la ligne verticale médiane la cible ou le distracteur aléatoirement, il a été possible d'isoler l'activité propre à la cible et au distracteur. Nos résultats suggèrent qu'il n'existe pas d'activité attentionnelle systématiquement liée aux distracteurs présents dans une scène de recherche visuelle. Ce résultat est particulièrement apparent quand on observe l'absence d'activité latéralisée pour les distracteurs vert lors de l'expérience durant laquelle la couleur cible change d'essai en essai. Cependant, on retrouve bien pour le distracteur rouge une P_D qui n'est pas présente pour les cibles rouges. Pourtant, l'apparence de la courbe de latéralisation du distracteur rouge suggère une grande similarité avec l'activité présente lorsque le rouge est cible. Il existerait donc possiblement sous certaines conditions une composante positive liée aux distracteurs, mais celle-ci pourrait bien être lié à un débalancement attentionnel entre le rouge et le vert. Le vert pourrait être un distracteur suffisamment faible en présence d'une cible rouge pour qu'aucun mécanisme attentionnel particulier ne soit engagé en sa présence. Une autre alternative serait qu'il existe une composante positive liée à tout item suffisamment saillant, mais que les composantes liées à la cible, soit la N2pc et la SPCN, provoquent une négativité qui masque partiellement cette positivité dans la condition ou la cible est latérale.

Le débalancement attentionnel entre le rouge et le vert s'observe à la fois au niveau des vitesses de réponses plus rapides et de la N2pc plus ample et plus hâtive pour le rouge. En

conservant la même couleur cible durant un bloc, nous avons tenté de renforcer les facteurs descendants en augmentant la stabilité d'un filtre de sélection basé sur la couleur cible. Il a été possible de réduire la différence d'amplitude entre les N2pc des deux couleurs cibles en changeant la couleur par bloc, mais les différences de vitesse de réponse et de latence de la N2pc sont demeurées. Cela laisse présager que les différences liées aux couleurs seraient liées en grande partie aux facteurs ascendants du système attentionnel.

Également, la Ppc qui accompagne à la fois les cibles et les distracteurs pourrait être lié au mécanisme de sélection et accompagnerait une présentation dont la saillance est inégale entre les hémichamps visuels. Le mécanisme de sélection d'une cible de couleur parmi des items gris provoquerait une sélection préattentionnelle des items de couleur. Ce mécanisme provoquerait une activité positive du côté où se retrouve l'item de couleur. On pourrait expliquer l'absence de Ppc pour le distracteur vert quand il n'est pas en bloc par une influence descendante insuffisante pour le renforcer comme item d'intérêt ou encore une saillance faible en contraste avec des items gris. Un item vert tel qu'observé dans le troisième chapitre ne semble pas se distinguer d'un item gris aussi aisément que le jaune et possiblement le rouge. Le fait que l'on peut manipuler la Ppc en faisant varier la couleur cible par bloc plutôt qu'aléatoirement démontre tout au moins qu'elle est sensible aux conditions imposées par la tâche et n'est pas purement sensible aux facteurs ascendants.

Les indices électrophysiologiques observés durant ce chapitre devraient encourager une certaine prudence dans l'utilisation des couleurs dans les expériences de recherche visuelle. Les résultats suggèrent que les couleurs ont des saillances attentionnelles différentes et qu'elles peuvent entrer en compétition avec les conditions imposées par la tâche pour déterminer le traitement attentionnel résultant. Malgré qu'il nous a été impossible de conclure sur l'existence d'une composante positive liée au distracteur, l'approche implicant de latéraliser soit la cible ou le distracteur semble utile pour départager leur activité spécifique.

Sur cette fondation, nous avons abordé l'activité attentionnelle en mémoire visuelle à court-terme dans le second chapitre en utilisant un paradigme semblable. En premier lieu, durant une tâche mémoire où une cible et un distracteur sont dans les hémichamps opposés, l'activité électrophysiologique observée après la présentation d'un indicateur de rappel au point de fixation visuel présente bien, tel qu'observé par Dell'Acqua (2010), une négativité contralatérale à la cible. Cette composante négative latéralisée, la TCN, se trouve à être plus antérieure que la N2pc et la SPCN couvrant le crâne au dessus du lobe temporal. Il est probable que la TCN représente des générateurs impliqués dans la récupération de l'information en VSTM distincts et antérieurs à ceux impliqués dans la sélection, l'encodage et la maintenance des représentations visuelles. Cette composante confirme qu'il existe bien une différence d'activité latéralisée entre les structures neuronales impliquées dans la rétention et la récupération de l'information visuelle en mémoire à court-terme en fonction de leur position relative aux items visuels qu'ils encodent. La nature latéralisée de cette composante suggère que les représentations en mémoire ont conservé, du moins en partie, les différences présentent entre l'hémichamps contralatéral et ipsilatéral à une cible lors de l'encodage en mémoire. La TCN bien que distincte de la N2pc et de la SPCN, représenterait un traitement attentionnel qui favoriserait la récupération de la cible. Cette activité est distincte de la SPCN, car cette activité a été éliminée par la ligne de base, mais cela n'écarte pas la possibilité que les même générateurs soit activés de manière plus importante durant la récupération.

Comme le traitement attentionnel représenté par la TCN repose sur une présentation comportant à la fois une cible et un distracteur latéral, nous nous somme intéressé à différencier l'activité liée à la cible de celle liée au distracteur. En utilisant un paradigme similaire à celui utilisé au premier chapitre, nous avons placé la cible et le distracteur sur la ligne verticale médiane lors de l'encodage. La topographie des potentiels sur le crâne lorsque la cible est latérale démontre bien que la TCN représente l'activité attentionnelle liée à la cible. On retrouve dans cette condition une composante négative antérieure qu'on ne retrouve pas lorsque le distracteur est latéral. L'absence de composante négative est consistent avec

l'absence de nécessité de récupérer l'information latérale lorsque le distracteur est latéral et que la cible se retrouve sur la ligne verticale médiane.

Pour sa part, le distracteur est accompagné d'une composante positive dans la région postérieure dont la topographie rappelle la SPCN. Cette composante pourrait représenter un mécanisme attentionnel d'inhibition de la représentation du distracteur en mémoire. Il y a également d'autres explications alternatives qu'il nous a été impossible d'écarter. Cette composante positive pourrait être un délestage de l'activité liée au maintien de l'information représenté par la SPCN lorsque l'indicateur confirme que l'item latéral est un distracteur. Comme la SPCN fait partie de la ligne de base, la disparition de cette activité serait observé comme une composante positive. Également, la région postérieure lorsque la cible est latérale tend vers le positif et l'activité mesurée à la pair d'électrodes d'amplitude maximale pour la composante positive suit un décours similaire à la pair d'électrodes d'amplitude maximale pour la composante négative. Cela pourrait suggérer une autre explication pour cette composante positive postérieure. Il pourrait s'agir d'une composante qui représente une activité attentionnelle liée à la sélection de la cible à récupérer en mémoire, à la manière de la Ppc pour la sélection d'une cible en recherche visuelle. Cette composante serait commune à la cible et au distracteur, mais la composante négative présente lorsque la cible est latérale pourrait venir couvrir et masquer en grande partie cette composante positive.

La soustraction des potentiels latéralisés liés au distracteur de ceux liés à la cible permet de vérifier que notre séparation des effets correspond bien à l'activité combinée de la cible et du distracteur lorsqu'ils sont présentés dans des hémichamps opposés. La courbe de différence correspond bien à la courbe obtenue avec une présentation balancée contenant un item dans chaque hémichamp à part durant la période de temps correspondant à la Ppc. Durant cette fenêtre de temps, la courbe de différence est plus positive que la courbe de la présentation balancée. Comme nous l'avons vu lors du premier chapitre, le fait d'avoir un item de couleur dans un seul des hémichamps produit un déséquilibre attentionnel qui est

observable par l'apparition d'une Ppc. Pour séparer l'effet de la cible et du distracteur, nous avons introduit un déséquilibre dans la scène visuelle avec un item de couleur dans un seul des hémichamps. Il est possible que ce qu'on observe ici est l'équivalent durant le rappel en mémoire de la Ppc pendant la perception. Ce serait donc une composante qui indique qu'il y a un déséquilibre attentionnel entre les hémichamps, mais ce débalancement se retrouve dans la représentation en mémoire de laquelle la cible est récupérée. Cet élément vient s'ajouter à la présence de la TCN pour confirmer une organisation latéralisé des structures impliquées dans le maintient et la récupération de l'information en mémoire visuelle à court-terme.

L'apparition d'une composante similaire à la Ppc lors du rappel d'information en mémoire suggère que les mécanismes attentionnels actifs durant la perception et la mémoire se ressemblent. La composante positive postérieure présente lorsque le distracteur est latéral durant la fenêtre de temps de la TCN est le prolongement de cette Ppc initiale et occupe une topographie similaire sur le crâne. Si on croit que la TCN masque partiellement la composante postérieure lorsque la cible est latérale durant un déploiement attentionnel vers les représentations mnésiques de la cible, on pourrait imaginer qu'un mécanisme similaire existe durant la perception. La composante N_T qui indique, durant la perception, un déploiement attentionnel vers une cible, pourrait être superposée à l'activité de la Ppc et de la P_D. Ainsi, l'activité liée au déséquilibre attentionnel (Ppc) et celle lié au distracteur (P_D) pourraient n'être d'une seule composante séparée en perception par la N_T. Durant la récupération en mémoire, la composante liée à la cible étant plus antérieur, elle ne viendrait pas se superposer aussi précisément sur le crâne à celle liée au distracteur ce qui laisserait un reliquat de composante visible dans la région postérieure.

Durant les deux premiers chapître, nous avons cherché à différencier l'activité propre au distracteur et à la cible. Dans le troisième chapitre, nous abordons l'effet électrophysiologique des distracteurs de moindre saillance lorsqu'ils sont dans le focus attentionnel. En utilisant une couleur commune à la cible et à un distracteur saillant, nous

avons établi une région d'intérêt attentionnel. Selon la théorie de la lentille attentionnelle, il est possible d'ajuster la taille du focus attentionnel aux demandes de la tâche. Comme la tâche requiert la combinaison de plusieurs caractéristique pour établir l'identité de la cible, un traitement attentionnel est requis pour identifier la cible parmi les deux items de couleur cible. Nous avons donc introduit des distracteurs gris à différents endroits pour vérifier leur effet en supposant que l'ajout de tels distracteurs aurait un effet différent qu'ils soit à l'intérieur ou à l'extérieur de la région couverte par le focus attentionnel.

Les résultats démontrent que les distracteurs gris perturbent le déploiement attentionnel tel qu'observé sur la N2pc, mais également dans la fenêtre de temps suivante occupée par la Ptc. L'ajout de distracteur gris augmente la difficulté d'identifier la cible en fonction de la position et du nombre de ces distracteurs gris, ainsi que de la couleur de la cible. En prenant une fenêtre de temps qui recouvre la période de la N2pc et de la Ptc, l'augmentation de l'activité liée à l'ajout de distracteurs à l'intérieur, à l'extérieur ou à l'intérieur et à l'extérieur de la zone d'intérêt attentionnelle créé par les items de couleur est la même. La distinction entre les différentes conditions se retrouve dans la distribution temporelle de cette activité. Les conditions qui créent une plus grande incertitude au niveau de l'identification de la cible ont une plus grande proportion de leur activité se retrouvant durant la Ptc et une plus petite durant la N2pc. L'inverse se produit pour les conditions qui introduisent moins d'incertitude.

Ainsi, la condition avec des distracteurs intérieur et la condition avec distracteurs intérieur et extérieur à la région d'intérêt ont une N2pc moins négative que la condition aux distracteurs extérieur. En contrepartie, en ajoutant les distracteur à l'intérieur et à l'extérieur on obtient une Ptc plus négative que pour la condition avec des distracteurs intérieur et la condition avec des distracteurs extérieurs. Entre les deux composantes, on observe donc un plus grand retard du déploiement attentionnel pour un nombre plus important de distracteur, mais particulièrement lorsque ceux-ci sont à l'intérieur de la région d'intérêt. On retrouve également ce délai dans la latence de la N2pc qui augmente avec l'ajout de distracteurs gris.

Un autre facteur qui accompagne un retard dans l'activité attentionnelle est la couleur cible. Les cibles jaunes semblent être plus facile à identifier par comparaison aux cibles vertes. La proportion d'activité repoussée dans le temps pour les cibles vertes est plus importante que pour les cible jaune lorsqu'on observe l'amplitude de la N2pc et de la Ptc. La latence de la N2pc pour une cible verte est aussi plus tardive que pour une cible jaune. Toutefois, au-delà de l'apparence des potentiels latéralisés différents, la soustraction de la condition sans distracteur gris des conditions avec des distracteurs gris permet de faire resortir à quel point l'effet observé est similaire pour le jaune et pour le vert. Le vert avait déjà été reconnu lors de notre premier chapitre comme moins saillant que le rouge. Notre interprétation avait alors été de voir le rouge comme particulièrement saillant, mais il semble que le vert soit également moins saillant que le jaune. Notre interprétation est que le vert est moins facile à distinguer des distracteurs gris que le jaune, car la condition sans distracteur gris ne comporte pas de différence notable entre le jaune et le vert à la fois au niveau des amplitudes et des latences. Pour vérifier que l'effet de couleur n'est pas lié à une compétition interhémisphérique entre les deux couleurs, nous avons fait une version de l'expérience qui ne comportait de la couleur que d'un seul côté. Comme nous n'avons pas trouvé de différence entre les deux versions de la tâche, il ne semble pas y avoir de raison de croire que l'effet de couleur observé est dû à la compétition attentionnelle entre jaune et vert.

L'influence du nombre de distracteurs gris, de la position des distracteurs et de la couleur cible se combine pour retarder l'activité attentionnelle. La manière dont le retard lié aux différents facteurs provoque un délai similaire en proportion variable plutôt qu'un retard variable et plus important pour les conditions les plus exigeantes suggère qu'on observe un mécanisme compensatoire sériel appliqué à chacune des cibles potentielles. Une possibilité serait qu'avec une difficulté accrue d'identifier la cible un nombre croissant de déploiement initial se ferait de manière fautive vers le distracteur et nécessiterait une redirection vers l'autre item. Cette hypothèse pourrait cependant difficilement expliquer que l'amplitude des

conditions plus exigeantes n'est pas plus importante que celle des conditions moins exigeantes dans la fenêtre commune incluant la N2pc et la Ptc.

Quelque soit le mécanisme qui est à l'oeuvre, nos observations de l'activité ayant lieu à l'intérieur de la fenêtre de la Ptc indiquent que cette période de temps peut servir à la prolongation des activités attentionnelles amorcées plus tôt durant la N2pc. Une interprétation de la Ptc comme un indicateurs de l'arrêt du déploiement attentionnel impliquerait que cette déflection positive devrait se trouver repoussée dans le temps ce qui ne semble pas être le cas. Cette hypothèse ne semble pas correspondre aux résultats obtenus à moins que cette interruption de déploiement attentionnel soit contrainte à une fenêtre de temps spécifique. De plus, il faut considéere que la Ptc se trouve entre deux composantes négatives, la N2pc et la SPCN, dont les variations d'amplitude peuvent également modifier l'amplitude de la Ptc qui les séparent. Il est donc fort risqué d'interpréter les variations de potentiel de cette composante sans considérer les explications alternatives.

Malgré l'innocuité apparente de l'ajout de distracteurs gris autour des cibles potentielles définies par la couleur cible, les effets attentionnels sur la N2pc et la Ptc se répercutent dans les processus plus tardifs tel l'encodage en mémoire de travail tel que suggéré par une latence plus tardive de la P3 pour les conditions avec plus de distracteurs gris. Il nous a même été possible d'établir un lien entre l'ajout de distracteurs gris et une réduction du taux de succès et une augmentation des temps de réponse.

Il est possible qu'une part des interractions entre les distracteurs gris et les cibles potentielles provienne de l'effet d'attroupement (ou « crowding ») causé par la proximité des distracteurs. Cependant, la présence de couleur devrait permettre de rompre l'effet d'attroupement en faisant ressortir les cibles potentielles. Il serait aussi difficile d'expliquer que les distracteurs à l'intérieur de la région d'intérêt causent un effet d'attroupement plus

important. Une autre explication possible serait que les distracteurs gris de par leur position favorisent des stratégies de recherche visuelles différentes. Un nombre croissant de distracteurs gris, rendant la tâche plus exigeante, pourrait encourager une recherche sérielle plus systématique. Bien que la cause de l'effet des distracteurs gris n'est pas évidente, les observations faites demeurent importantes pour comprendre les mécanismes attentionnels mis en oeuvre lors d'une recherche visuelle pour compenser une incertitude croissante pour l'identification d'une cible.

Une vue d'ensemble de nos résultats souligne la grande souplesse des mécanismes attentionnels dans l'identification de cible et de distracteurs. Ainsi, un distracteur ne semble pas nécessairement requérir de traitement attentionnel, pourtant même un distracteur gris qui ne partage pas la couleur cible peut interférer avec le déploiement de l'attention. Il existe donc différents mécanismes pour identifier une cible parmi des distracteurs. Un mécanisme d'inhibition des distracteurs ne semble être présent que lorsque la saillance d'un distracteur est exceptionnelle, allant au-delà du simple « pop-out » de couleur. De plus, un tel mécanisme d'inhibition risque d'être confondu avec d'autre mécanismes liés à la perception si l'observation d'un tel mécanisme requiert un débalancement des propriétés physiques visuelles de la présentation. Quant aux effets des distracteurs de notre troisième chapitre, il semble qu'ils découlent de notre paradigme particulier. Malgré une très faible saillance liée à leur couleur, ces distracteurs occupent l'espace voisin de la cible ce qui augmente leur chance d'interférer avec la tâche. La recherche d'items similaires entre cible et distracteurs à l'intérieur d'un faisceau attentionnel large entraîne un retard important du déploiement attentionnel. Une inclusion involontaire de distracteurs à l'intérieur du faisceau attentionnel pourrait avoir pour effet de supprimer en partie l'avantage que procure l'attention à la recherche visuelle.

La dualité apparente de la cible et du distracteur semble reposer sur un continuum qui n'est pas aussi aisément défini qu'il ne le paraît. La manipulation des différents facteurs pourrait mener à différentes stratégies et mécanismes attentionnels ajustés à la tâche. Notre

approche pour séparer l'activité liée à la cible de celle liée au distracteur a ses limites. D'abord, l'influence d'un distracteur sur l'activité propre à la cible sera toujours observable du côté de la cible, même si le distracteur est sur la médiane verticale. On pourrait tenter de faire la différence entre l'activité lorsqu'un distracteur est sur la médiane verticale et la cible latérale d'une autre condition où seule la cible est présente, mais il est possible que le retrait du distracteur vienne changer le traitement attentionnel. Également, les mécanismes attentionnels impliqués durant l'identification de la cible en recherche visuelle sont dépendant de la stratégie adoptée. Comme cette stratégie est liée à la tâche, il est incertain que le paradigme de sépararation de l'activité de la cible et du distracteur nous permet de conclure pour tout paradigme de recherche visuelle. De plus, il est possible que durant la recherche visuelle un distracteur soit par erreur traité comme une cible et vice-versa. Ceci aurait pour conséquence d'ajouter du bruit à nos mesures, à moins que des conditions particulières viennent rendre ce traitement erroné systématique. Ceci pourrait, par exemple, provoquer l'apparition d'activité lié à la cible dans la condition avec un distracteur latéral. Ces différentes limitations sont autant de questions qui devront être résolues éventuellement.

Dans l'immédiat, certaines questions se posent pour mieux comprendre à la fois les composantes électrophysiologiques et l'attention visuelle et plusieurs avenues de recherche s'ouvrent à nous. Tout d'abord, il serait intéressant de voir s'il existe une différence entre les participants qui ont plus de succès à compléter une tâche de recherche visuelle et ceux pour qui la tâche est plus difficile. Ceci pourrait nous permettre d'explorer la question des stratégies de recherche visuelle. Peut-on faire autrement et potentiellement mieux dans notre identification d'une cible. Vérifier la capacité pour un participant d'adopter une stratégie différente pour une tâche identique serait intéressant pour le débat de l'importance relative des facteurs ascendants et descendants. Il serait intéressant aussi de voir s'il est possible pour un participant de modifier volontairement son approche. Ensuite, il serait important d'identifier l'activité à laquelle est rattachée la Ptc lorsqu'elle n'est pas occupée par l'activité de la N2pc. Elle pourrait représenter l'activité liée à un distracteur comme la P_D, l'activité liée à la terminaison du déploiement attentionnel ou encore une prolongation de la Ppc masquée en

partie par la N2pc. Enfin, il serait intéressant de s'attarder à l'effet des distracteurs gris observé lors du troisième chapitre. Il serait intéressant de voir s'il s'agit d'un effet attribuable à l'attroupement. Celà pourrait permettre d'éclairer la manière dont l'attention réduit l'incertitude entre items voisins ou encore l'activité électrophysiologique indiquant qu'elle ne parvient pas à identifier la cible.

Dans l'ensemble, nous avons utilisé l'activité électrophysiologique liées aux cibles et aux distracteurs pour mieux comprendre les mécanismes attentionnels. Malgré la simplicité apparente des tâches, il appert que l'identification et le traitement attentionnel de cibles requiert des mécanismes variables. Il ne semble pas y avoir d'inhibition systématique des distracteurs. Les mécanismes attentionnels sont plus subtils et ne semblent pas ignorer systématiquement les distracteurs. Aussi, il semble que des mécanismes attentionnels similaires soit présent en perception et en mémoire pour distinguer une cible d'un distracteur. Un item qui était une cible à l'encodage, possède une représentation latérale en VSTM qui est un distracteur quand viens le temps de récupérer un seul des deux items encodés. Les mesures électrophysiologiques font ressortir des différences et des raffinement expérimentaux intéressants, mais leur interprétation demeure complexe. Une interprétation personnelle de l'histoire que semble raconter ces résultats est que l'attention visuelle ne gère pas les distracteurs, elle ne fait que se préoccuper des potentielles cibles. Comme l'attention visuelle intervient au cours d'un processus incrémental d'acquisition d'information à propos d'une scène visuelle, il n'y a pas de distracteurs *a priori* que des cibles potentielles. Si les informations visuelles acquises très tôt permettent d'éliminer un item comme une cible potentielle, aucun mécanisme attentionnel particulier ne sera requis pour son traitement. Par contre, si la stratégie de recherche adoptée, la scène de recherche visuelle ou encore une quantité insuffisante d'information connue sur la cible et sur les distracteurs à un moment critique ne permet pas d'écarter un item, il sera traité comme cible. Les cibles et les distracteurs ne sont probablement pas destinés à vivre heureux et à avoir beaucoup d'enfants; l'attention visuelle veille à cela.

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